THE
INDIAN ZOOLOGICAL MEMOIRS

ON

INDIAN ANIMAL TYPES

EDITED BY

K. N. BAHL, D.Sc., D.Phil., F.R.A.S.B.

VII

SALMACIS

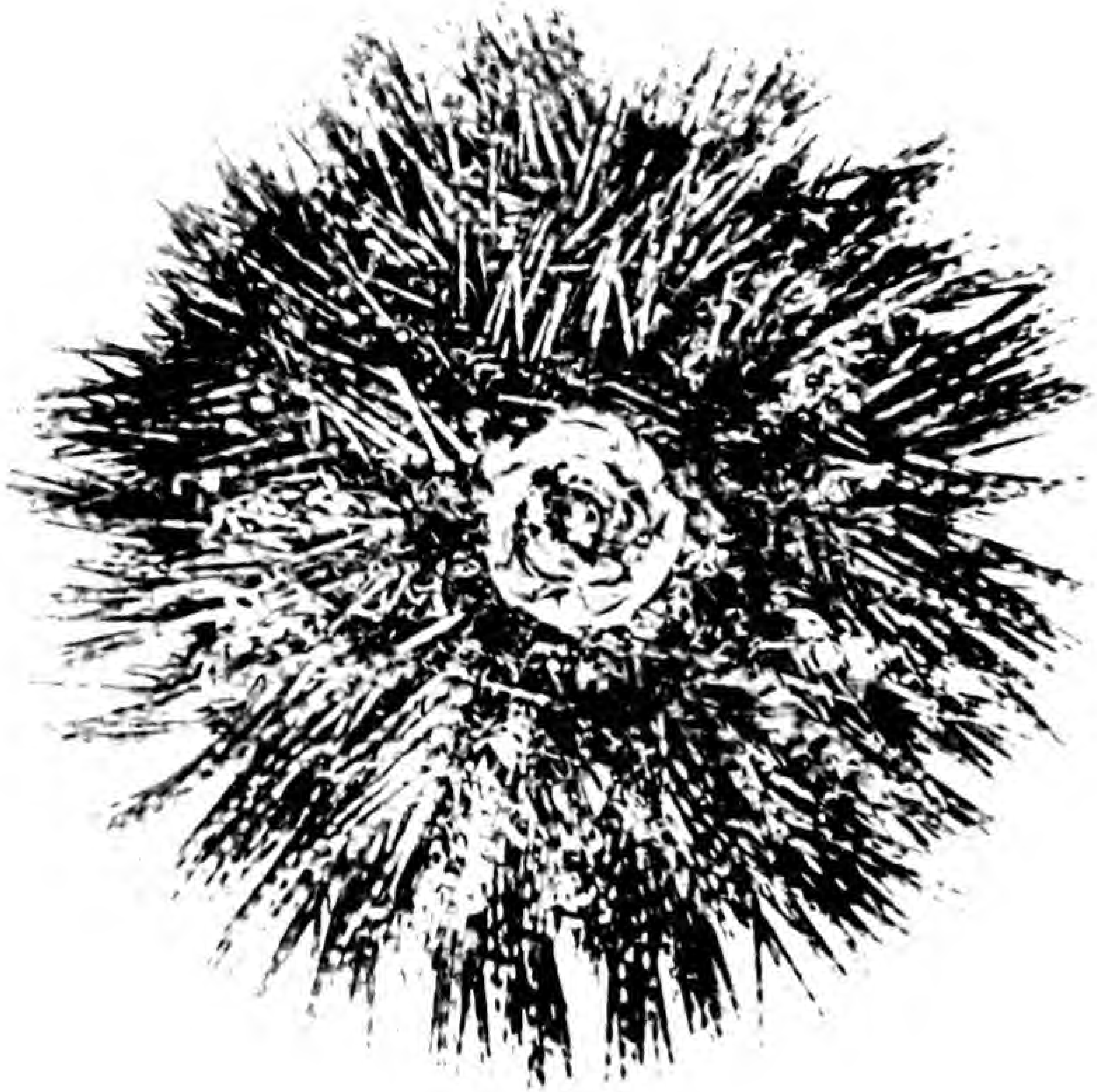
(*THE INDIAN SEA-URCHIN*)

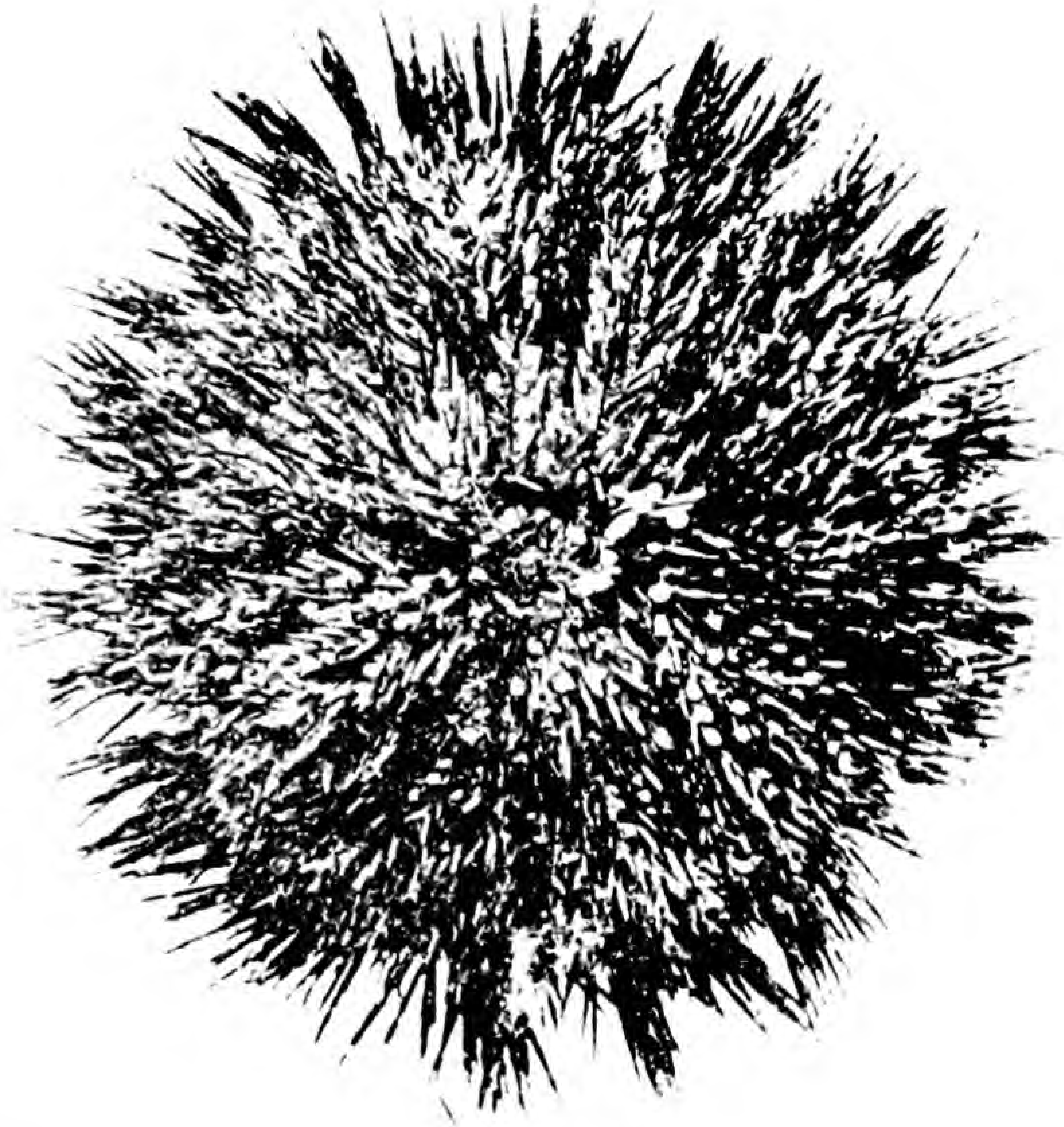
BY

R. GO[illegible]YAR, M.A., M.Sc.
Pro[illegible]r of Zoology,
Unive[illegible]of Madras

With Frontispiece and 47 Text-Figures

Lucknow Publishing House
LUCKNOW
April, 1938


Oral view


Aboral view

SALMACIS BICOLOR

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First Edition, 1938

Printed and published by C. O. Forsgren
at the
Lucknow Publishing House, Lucknow

EDITOR'S PREFACE

Zoology as a subject in the university curriculum is becoming increasingly popular with students in India, but there are hardly any books that deal with the structure and development of common Indian animals. While our students dissect the Indian types, they still use British text-books which are naturally based on the British fauna. The need, therefore, of books describing common Indian animal forms has been keenly felt in our zoological laboratories.

In my Presidential Address to the Zoology Section of the Indian Science Congress at Bangalore (1924), I suggested that a series of memoirs on Indian animal types should be prepared and published along the lines of the excellent series issued by the Liverpool Marine Biology Committee under the editorship of the late Sir William Herdman. The suggestion has been taken up by a committee of zoological workers who have decided to issue a series of monographs under the title of "The Indian Zoological Memoirs". The committee have selected the following types for the series and have assigned them to various workers. Memoir I was published in 1926, Memoir II in 1928, Memoir III in 1931, Memoir IV in 1932, and Memoir V in 1936. A second edition of Memoir I was also published in 1936, Memoir VI appeared in 1937, Memoir VII is appearing now, and it is hoped that other memoirs will follow soon.

I. The earthworm *Pheretima*, K. N. Bahl (*Second Edition*), pp. 85, figs. 45.
II. The shark *Scoliodon*, Miss E. M. Thillayampalam, pp. 116, figs. 42.
III. The Bombay oyster *Ostrea cucullata*, P. R. Awati and H. S. Rai, pp. 107, figs. 51.
IV. The apple-snail *Pila*, Baini Prashad, pp. 83, figs. 43.
V. The monascidian *Herdmania*, S. M. Das, pp. 103, figs. 64.
VI. The prawn *Palaemon*, S. S. Patwardhan, pp. 100, figs. 65.
VII. The sea-urchin *Salmacis*, R. Gopala Aiyar, pp. 69, figs. 47.
VIII. The leech *Hirudinaria*.
IX. The Indian carp *Labeo rohita*.
X. The centipede *Scolopendra*.
XI. The millipede *Thyropygus*.

XII. The starfish *Pentaceros.*
XIII. The sting-ray *Trygon.*
XIV. The scorpion *Palamnaeus.*
XV. The Sipunculid *Dendrostoma.*

In addition to these, other memoirs on suitable types will be arranged for, as finances permit.

The committee gratefully acknowledge a donation of Rupees seven hundred made by the editor and of Rupees thirty made by some of his students towards the cost of publication of these memoirs. They also wish to express their indebtedness to Mr. C. O. Forsgren, the Agent of the Lucknow Publishing House, for his continual advice and help in the production of these memoirs.

My best thanks are due to Prof. E. W. MacBride who at my request kindly looked through the text of this memoir and made very helpful suggestions. Dr. S. M. Das has kindly helped me in looking through the proof-sheets and Mr. M. L. Bhatia has been very helpful with the illustrations.

K. N. BAHL

University of Lucknow,
April, 1938.

AUTHOR'S PREFACE

Every teacher of Zoology in this country deplores the absence of proper manuals on Indian animal types. Our students are more familiar with the structure and life-histories of European forms of life than with those of Indian forms. The series of Indian Zoological Memoirs founded by Professor K. N. Bahl fills a long felt want, and so when he asked me to write a memoir on *Salmacis bicolor*, I readily consented. This urchin is extremely common along the Indian coast and can be easily obtained from the Madras Fisheries Station at Ennur. It is of a convenient size for the anatomy to be made out without any difficulty. As the work progressed I realised that it was necessary to work out the development to make the memoir complete. The description of the development is based on observations made on larvae artificially cultured in this laboratory, where it has been possible to rear the larvae considerably beyond the stage of metamorphosis and to keep them alive for months. It is hoped that the memoir will be found useful to both teachers and students in the Indian universities.

I have great pleasure in thanking Professor E. W. MacBride for going through the manuscript and making several useful suggestions. My best thanks are due to the editor, Professor K. N. Bahl, who has critically revised both the text and the illustrations and has taken great pains in editing the memoir and seeing it through the press.

Department of Zoology,
University of Madras,
April, 1938.

R. GOPALA AIYAR

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CHAPTER I

INTRODUCTION

The Echinodermata (Gk. *ekhinos*, hedgehog; *derma*, skin: spiny-skinned animals) are coelomates which exhibit in the adult condition a radial symmetry in their external as well as in most of their internal organs. The skeleton is mesodermal and takes the form of definitely arranged calcareous plates or scattered spicules. The perivisceral cavity is coelomic. A peculiar system of coelomic origin, known as the water vascular system, is always present. Locomotion is brought about either by the tube-feet controlled by the water vascular system, or by the flexion of the arms or by the contractions of the body-wall. The nervous and vascular systems have a pentamerous arrangement and consist mainly of a circum-oral ring with radiating strands or tubes. A special excretory system is absent. The sexes are separate and the gonads usually occur in the form of five bunches having independent openings to the exterior. There is usually a well-developed pelagic larva showing bilateral symmetry which undergoes a remarkable metamorphosis resulting in the radial symmetry of the adult. Regeneration of lost parts is very common.

The phylum Echinodermata includes the starfishes, the brittle-stars, the sea-urchins, the sea-cucumbers, and the sea-lilies or feather-stars. They are all essentially marine, only two species of Holothuroidea having been recorded from brackish water and none from fresh water. *Synapta similis* enters the brackish water in the mangrove swamps of the tropics, while the other Holothurian *Haplodactyla molpadioides* has been obtained at the mouth of the Ganges [1]. Echinoderms are cosmopolitan in their distribution, being found in all seas.

Early zoologists like Cuvier placed the Echinodermata together with the Coelenterata as members of a larger group called the Radiata. But when it was realized that the Echinoderms are coelomates and have a distinct gut with a spacious coelom surrounding it, they were separated by R. Leuckart from the Coelenterata and now form an independent phylum.

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1 Annandale, N.—"The marine element in the fauna of the Ganges". Bijdr. t. Dierk, Amsterdam, Vol. 22, 1923.

PHYLUM ECHINODERMATA[1]

Sub-phylum I. ELEUTHEROZOA.

Echinoderms that move freely during their adult life, but may remain fixed for a short period during their larval stage by a stalk arising from the *oral* surface.

Class I. *Asteroidea* (Starfishes).

Body star-shaped or pentagonal, often attaining large dimensions. Central disc not sharply separated from the arms. Arms usually five. Body dorso-ventrally depressed. Mouth 'oral' and anus 'aboral' in position. Ambulacral grooves open and bordered by tube-feet which usually bear suckers. Skeleton well-developed. An inter-radial madreporite present on the aboral side. Stomach large and sac-shaped, succeeded by a pentagonal sac bearing long tubular diverticula which extend into the arms; intestine short and anal opening small or absent. Pedicellariae two-bladed. Larva known as *Bipinnaria.* Starfishes are always carnivorous, often gregarious.

COMMON INDIAN FORMS :—*Astropecten indicus*, *Asterina coronata*, *Pentaceros hedemanni*, *Luidia maculata*, *Linckia laevigata*, *Oreaster lincki*, *Palmipes sarasini*, etc.

Class II. *Ophiuroidea* (Brittle-stars).

Disc small, surface leathery. Arms usually five in number, sharply marked off from the central disc, and branched in one sub-division of the class. Mouth oral; anus absent. Skeleton well-developed, consisting of a system of arm-ossicles and body-plates. Movement by rapid flexion of the arms. Ambulacral grooves closed. Tube-feet without suckers; pedicellariae absent. Larva known as *Ophiopluteus.* Brittle-stars feed on the organisms contained in the mud at the bottom of the sea, chiefly on small molluscs and worms. Many possess remarkable powers of self-mutilation and regeneration of lost parts. They are commonly found in the mud in enormous numbers and are of importance in the economy of the sea, often limiting the spread of other organisms whose young they devour.

COMMON INDIAN FORMS :—*Ophiohela danae*, *Ophiactis savignyi*, *Ophiophragmus relictus*, *Ophiocoma scolopendrina*, *Ophiothrix hirsuta*, *Gorgonocephalus levigatus*, *Pectinura conspicua*, etc.

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1 The classification adopted in this memoir is mainly based on that given by MacBride in the Cambridge Natural History, Vol. 1, 1909.

Class III. *Echinoidea* (Sea-Urchins).

Form globular, heart-shaped or cake-shaped; no free arms. Skeleton well developed, consisting of a compact system of ten zones of rigidly arranged plates. Mouth oral; anus aboral. Ambulacral grooves closed and running like meridians of longitude over the body. Moveable complicated jaw-apparatus present in the globular forms. The alimentary canal a simple tube with a complicated course. The regular urchins frequent rocks, while the cake-urchins and heart-urchins are found on sandy bottoms. Larva known as the *Echinopluteus* which is very similar to the Ophiopluteus.

COMMON INDIAN FORMS:—(1) Regular Urchins:—*Salmacis bicolor*, *Stomopneustes variolaris*, *Temnopleurus toreumaticus*, etc. (2) Cake-Urchins:—*Echinodiscus auritus*, *Clypeaster humilis*, etc. (3) Heart-Urchins:—*Laganum decogonale*, *Lovenia elongata*, *Echinolampas oviformis*, etc.

Class IV. *Holothuroidea* (Sea-cucumbers).

Echinoderms having a sausage-shaped or worm-like appearance. Oro-anal axis parallel to the substratum. Free arms absent. Skeleton greatly reduced, consisting of small ossicles round the gullet and a variety of spicules in the muscular body-wall. Ambulacral grooves closed and running longitudinally down the body from the mouth to the anus. Alimentary canal tubular and coiled, always with a ring of tentacles round the mouth, which are modified and enlarged tube-feet. Characteristic cloacal appendages known as *respiratory trees* and *Cuvierian organs* present in most of the typical members of the class. Gonad single. Larva known as the *Auricularia*. Mutilation of internal organs very common. Some break up into pieces on irritation. Holothurians are usually creeping and burrowing in their habit, but a few forms like *Pelagothuria* and *Planktothuria* are pelagic.

COMMON INDIAN FORMS:—*Actinocucumis typica*, *Holothuria scabra*, *Stichopus chloronotus*, *Cucumaria conjungens*, *Synaptula recta*, etc.

Sub-phylum II. PELMATOZOA.

Echinoderms which are attached throughout life or during the larval period by a fixing organ or stalk arising from the *aboral* surface.

Class *Crinoidea* (Feather-stars or Sea-lilies).

Arms feather-like, radiating from a central cup. Oral side turned upwards. Ambulacral grooves open. Tube-feet finger-like, never bearing suckers. Mouth and anus on the oral side. Fixation may be temporary or permanent. The permanently attached forms live in deep sea. Larva resembles externally the 'pupa' of a Holothurian and passes through a pentacrinoid stage.

COMMON INDIAN FORMS (Free-living when adult) :— *Tropiometra encrinus*, *Oligometra serripinna*, *Lamprometra palmata*, *Heterometra reynaudi*, etc.

There are three other classes (*Cystoidea*, *Blastoidea*, and *Edrioasteroidea*) included under the sub-phylum Pelmatozoa but, all the members of these classes are fossil forms and are therefore not listed here.

The class ECHINOIDEA includes the following three orders:

Order 1. *Endocyclica* (Regular Urchins).

Peristome central on the oral surface; periproct central on the aboral surface and surrounded by the apical system of plates. Lantern apparatus present. Branchiae external or internal. Anus within the apical system.

Order 2. *Clypeastroidea* (Cake-Urchins).

Extremely flattened forms living in sand, often pentagonal in shape. Mouth central or sub-central. Anus outside the apical skeleton in the posterior inter-ambulacrum. Special gills as are found in the Endocyclica are not present. There are no compasses (radii) in the lantern apparatus. Tube-feet of different kinds in one and the same animal. In the aboral portions of the ambulacra the plates are enlarged so that this portion looks like the petals of a flower. The enlarged plates bear large basally flattened tube-feet which act as gills.

Order 3. *Spatangoidea* (Heart-Urchins).

Test more or less heart-shaped. Mouth central or excentric. Anus outside the apical system in the posterior inter-radius. External gills and lantern apparatus absent. Ambulacra often form apical petaloids like those of the Clypeastroidea. All are burrowers in the sand or mud at the bottom of the sea.

The *Endocyclica* [1] are divided into *eleven* families:—

Family 1. *Cidaridae.* Endocyclica with large peristome and periproct, the former covered by a regular series of both ambulacral and inter-ambulacral plates. The ambulacral plates bear a series of small tube-feet. External gills absent. Stewart's organs well developed. Test stout with relatively few plates in each ambulacral column. Each inter-ambulacral plate bearing one primary spine. No spines on the ambulacral plates. Primary tubercles perforate.

Family 2. *Echinothuridae.* Endocyclica with a large peristome and comparatively small periproct. Peristome with only a regular series of ambulacral plates pierced by small tube-feet. No specially modified buccal tube-feet. External as well as internal gills (Stewart's organs) present. Coronal plates separated by thin flexible strips of body-wall. Ambulacral plates compound.

Family 3. *Saleniidae.* With large peristome and periproct, the former covered with thin scattered irregular plates. External gills and five pairs of special buccal tube-feet are present. Ambulacral plates mostly simple. Periproct with a permanent large suranal plate.

Family 4. *Stomopneustidae.* Teeth keeled. Primary tubercles imperforate. Ambulacral plates compound, composed of three primary plates, but in the mid-zone every four or five such plates are united and overgrown by a large primary tubercle.

Family 5. *Arbaciidae.* Peristome with ten prominent plates which are perforated by buccal tube-feet, along with thin irregular plates which are not perforated. External gills present. Auricles consist of incomplete arches springing from the ambulacral plates; these plates are compound, with three to five primary plates in each plate. Periproct covered by four valve-like plates.

Family 6. *Diadematidae.* Peristome as in Saleniidae and Arbaciidae. External gills and buccal tube-feet present. Periproct small, covered with numerous small plates. Auricles form complete arches. Rudimentary Stewart's organs present. Ambulacral plates compound. Peristome not plated.

Family 7. *Aspidodiadematidae.* Most of the characters as in the previous family, but the ambulacral plates simple and the

1 This classification, though mainly based on that given by MacBride in the Cambridge Natural History, has been modified following Clark. The family Echinidae as given in the Cambridge Natural History has been split up into Echinidae, Strongylocentrotidae, Echinometridae, and Temnopleuridae; while the families Stomopneustidae and Aspidodiadematidae have been added.

coronal plates thin; oculars large and all insert; peristome leathery and only partially plated.

Family 8. *Echinidae* [1]. External gills and buccal tube-feet present, but Stewart's organs absent. Peristome and periproct as in Diadematidae; the plates meet each other in straight simple sutures. Test without sculpturing or pits. Ambulacral plates with typically three elements.

Family 9. *Strongylocentrotidae* [1]. Test as in Echinidae. Ambulacral plates compound with four or more elements (rarely 3).

Family 10. *Echinometridae*. Test as in Echinidae. Ambitus more or less elliptical. Ambulacral plates compound with 3-19 elements, but usually more than four. Oculars all exsert or becoming insert in the sequence V, I, IV, not the usual arrangement of I, V, IV.

Family 11. *Temnopleuridae*. Similar to the Echinidae in many features. Plates of the corona dovetail into each other by means of pits and knobs along the line of suture. Ambulacral plates compound with three elements; pits or sculpturing on coronal plates dorsally; ocular plates all exsert.

Key to the Indian Genera of the Family Temnopleuridae

Only two genera, *Salmacis* and *Temnopleurus*, have been recorded from the Indian coasts, and of these, *Salmacis* is the commoner form. The two genera are distinguished as follows:—

1. Test with pits; primary tubercles crenulate; each coronal plate at ambitus with 1-3 (rarely 4) primary tubercles. ....*Temnopleurus*.
2. Test with pits; primary tubercles crenulate; each coronal plate at ambitus with 4-9 primary tubercles. ....*Salmacis*.

Genus *Salmacis* Agassiz.

Test high or somewhat flattened. Tubercles crenulate; Each coronal plate at ambitus with 4-9 primary tubercles.

Salmacis is a very common sea-urchin and ranges through the tropical areas of the Pacific, the Atlantic, and the Indian Oceans. It has long been noted that species of *Salmacis* are

1 Prof. MacBride informs me that it is doubtful whether these two families can be validly distinguished from each other.

difficult to identify from one another. Clark in his Catalogue of the Recent Sea-Urchins (1925) mentions seven species and a variety, namely, *S. belli*, *S. bicolor*, *S. dussumieri*, *S. erythracis*, *S. rubricincta*, *S. sphaeroides*, *S. virgulata*, and *S. virgulata var. alexandri*. Of these, *S. bicolor*, *S. sphaeroides*, *S. virgulata* and *S. dussumieri* occur along the Indian coasts. The first two are common in the Madras Harbour and may be obtained at any time of the year; both are brightly coloured, but *S. bicolor* has more of yellow colour on the spines, and grows to a slightly larger size than the other species. Besides, it can be distinguished by the possession of two distinct types of globiferous pedicellariae, while *S. sphaeroides* has only one type. The only other species of *Salmacis* with two types of pedicellariae is *S. belli* but this is mainly an Australian form[1].

Key to the species of Salmacis *known to occur along the Indian coast*

1. Globiferous pedicellariae of two kinds; large ones mostly apical without lateral teeth; small ones of uniform distribution, with an unpaired lateral tooth. Tridentate pedicellariae with short broad valves. Spines ringed. Tubercles occur outside the pores. ......*S. bicolor*, Ag.

Globiferous pedicellariae of one kind, with or without 1-1 lateral teeth. Spines ringed or not. Tridentate pedicellariae with narrow blades. ......2.

2. Globiferous pedicellariae without lateral teeth. Spines not ringed. No tubercles outside the pores. ......*S. virgulata*, Ag.

Globiferous pedicellariae with 1-1 lateral teeth. Tubercles outside the pores. ......3.

3. Test rather high; peristome not much sunken. A primary tubercle is found on each ambulacral plate. ......*S. sphaeroides*, Ag.

Test very low; peristome much sunken. A primary tubercle is found on every second ambulacral plate. ......*S. dussumieri*, Ag.

1 *S. rubricincta* Clark, recorded from Saya de Mahl, Indian Ocean, has much in common with *S. bicolor*, but can be easily distinguished by the difference in colour. In *S. rubricincta* the primary spines are white with red rings, and the small spines are completely white, whereas in *S. bicolor* the spines have red bases and the small ones are bright red.

CHAPTER II

EXTERNAL CHARACTERS

The body of *Salmacis* is more or less globular in shape, being distinctly flattened at one pole and conical at the other. The flattened pole is distinguished as the *oral* or *actinal pole*, while the conical pole is called the *aboral* or *abactinal* pole. A fair sized specimen has a diameter of about 70 mm. at its widest part and a height of about 45 mm. from the oral to the aboral pole. At the centre of the oral pole there is a circular opening, the *mouth*, through which project the free ends of five ivory-white file-shaped *teeth*. Surrounding the mouth there is a circular area of soft skin, the *peristome* or *peristomial membrane* (fig. 1), which looks like the iris of the vertebrate eye; the peristome exhibits two distinct areas, an inner brownish and an outer whitish; the inner immediately surrounding the mouth is thick and muscular and is characterised by the presence of radiating ridges and grooves all over its pigmented surface, while the outer area is smooth and membranous. Close to the periphery of the inner area the peristome bears five pairs of special tube-feet called the *buccal tube-feet* or *oral tentacles* which are radial in position. Just outside the peristome, amongst the spines, are situated five pairs of branched fleshy structures called the *dermal branchiae*; they also lie in five groups, but, unlike the oral tentacles, are inter-radial in position. At the aboral pole there is a very small aperture, the *anus*, which is surrounded by an area of leathery skin called the *periproct*.

The entire surface of the body except the peristome and the periproct, is covered by a forest of large *spines* which, in a living sea-urchin, are actively movable and help in the locomotion of the animal. It is the presence of these spines that gives the name Echinoidea (Gk. *ekhinos*, a hedgehog) to the class to which the sea-urchin belongs. In *Salmacis bicolor* the spines are slender and are not strong enough to bring about rapid movements of the body as in the case of forms like *Stomopneustes* in which they are very strongly developed. Each spine is cylindrical in shape but pointed at its distal extremity; it is solid in texture and its outer surface is longitudinally fluted (fig. 3). In a living specimen the spines are brilliantly coloured, the longer ones

being banded alternately red and yellow and usually bright red at the base, while the smaller spines are mostly bright red. It is a pretty sight to see the animal moving slowly along on its spines with the help of the tube-feet. The basal or proximal end of each spine has a cup-shaped concavity which fits over a raised *tubercle* on the skeleton of the body, thus forming a "cup and ball joint" (fig. 3). As the tubercle is larger than the base of the spine, the spine has a large range of movement. Around the base of the

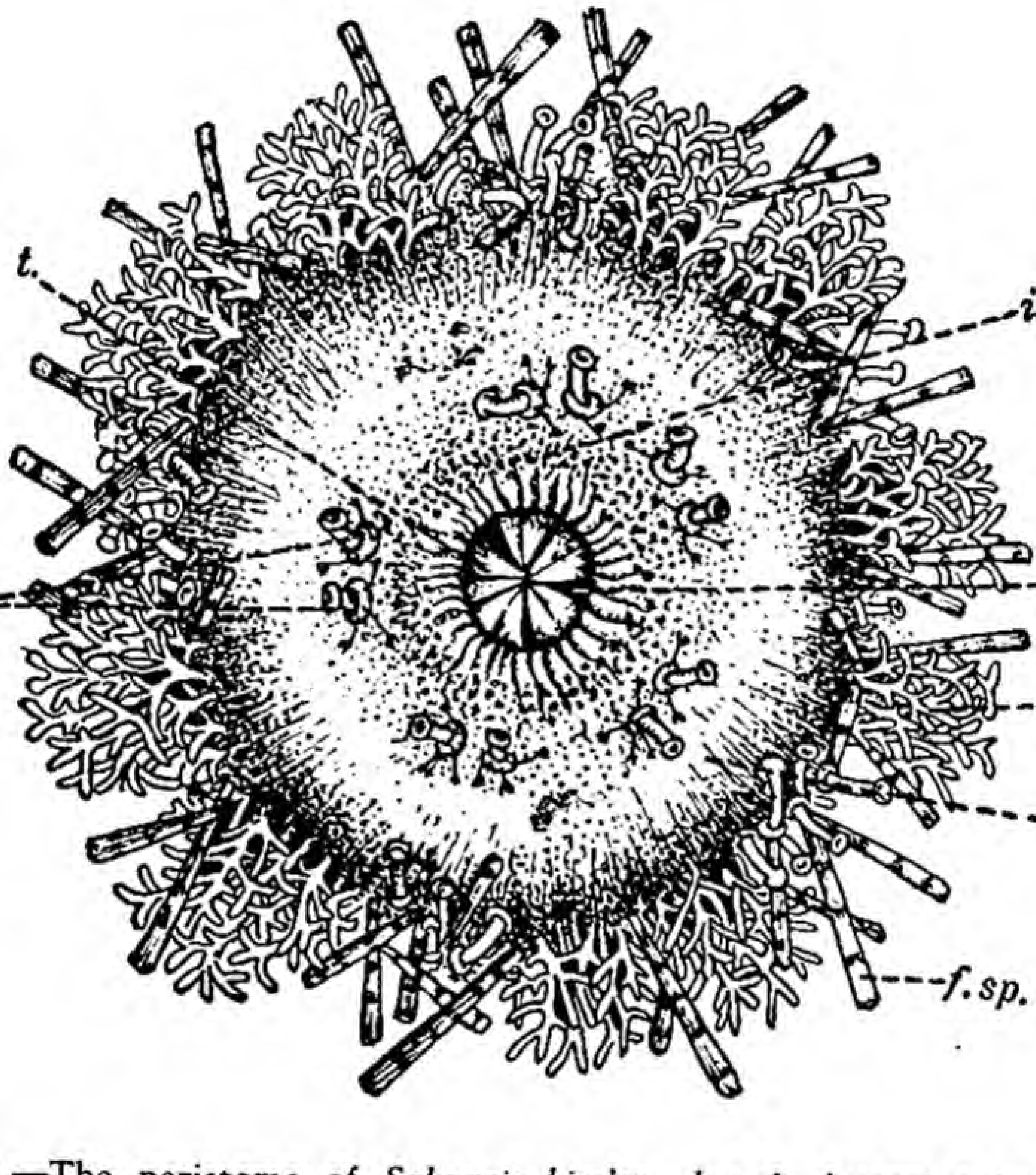


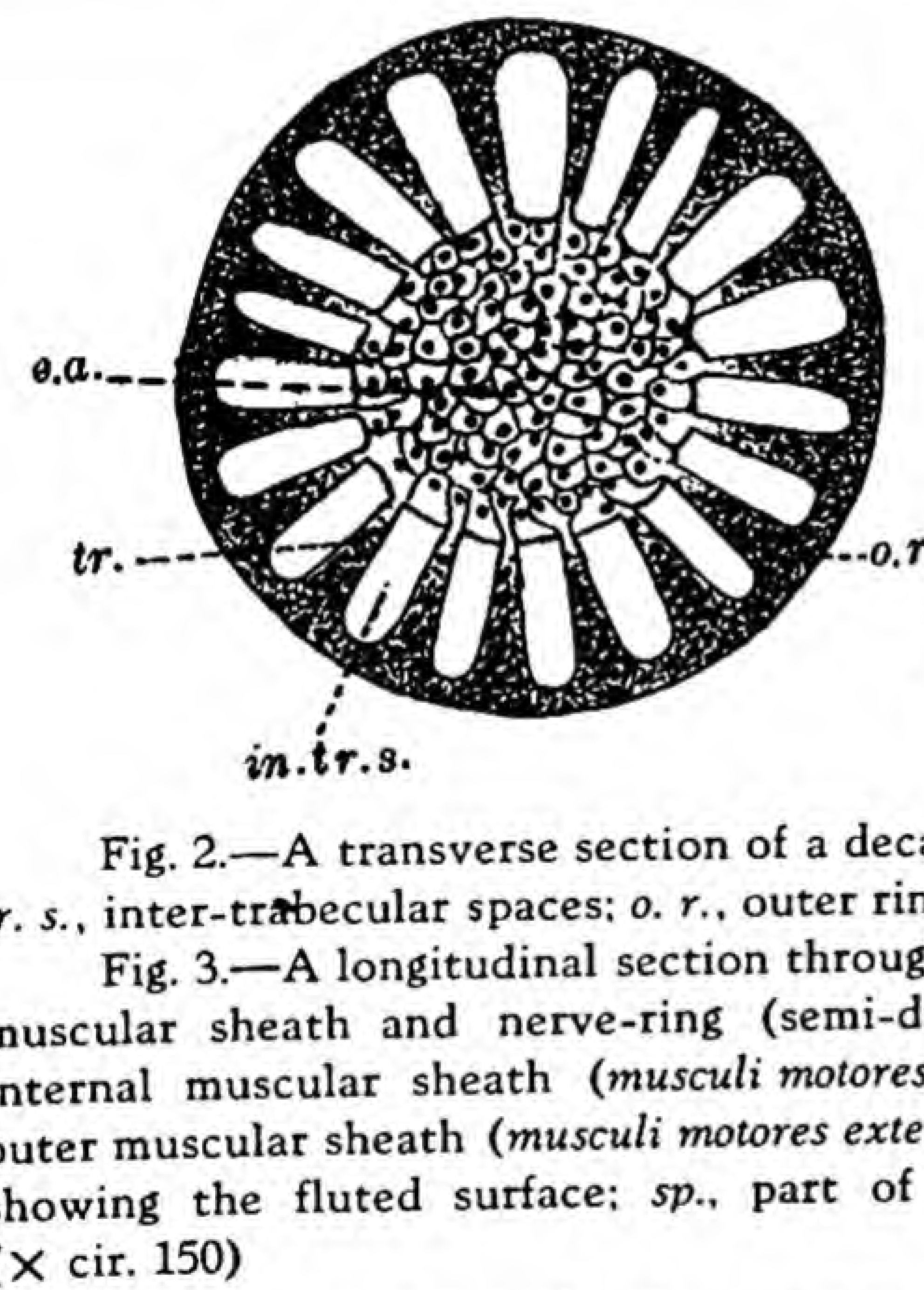
Fig. 1.—The peristome of *Salmacis bicolor*. *b. t. f.*, buccal tube-feet; *br.*, branchiae; *f. sp.*, flattened spine; *i. p.*, inner area of peristome; *mth.*, mouth; *o. p.*, outer area of peristome; *t.*, teeth. (× cir. 3½)

spine there is a rough circular ridge formed of a ring of minute projections; the base and this ridge of the spine are connected with the tubercle by a cylindrical sheath of muscle-fibres, by the contraction of which the spine may be moved about or rotated in any direction. The muscular sheath (fig. 3) consists of an outer and an inner layer; the outer layer called the *musculi motores externi aculei* consists of strong translucent fibres, while the muscles of the inner layer, the *musculi motores interni aculei*, are opaque-white and form a kind of ligamentous sheath. The

muscles of the outer layer are easily stimulated and are capable of vigorous contraction, by means of which they bring about the movements of the spines. The muscles of the inner layer, however, need a strong stimulus to contract; but once contracted, they can remain so for a long period; their function seems to be to hold each spine firmly in position; these muscles have therefore been called "block muscles" by Uexküll.

The muscular sheath, like the surface of the body, is covered with a ciliated ectoderm. A nerve-ring underlying the ectoderm surrounds the muscular sheath and stimulates it to contract (fig. 3).

The muscle-fibres are smooth and non-striated. Each muscle-fibre is frayed out at its two ends and possesses a nucleus in the middle of its length surrounded by a little cytoplasm.



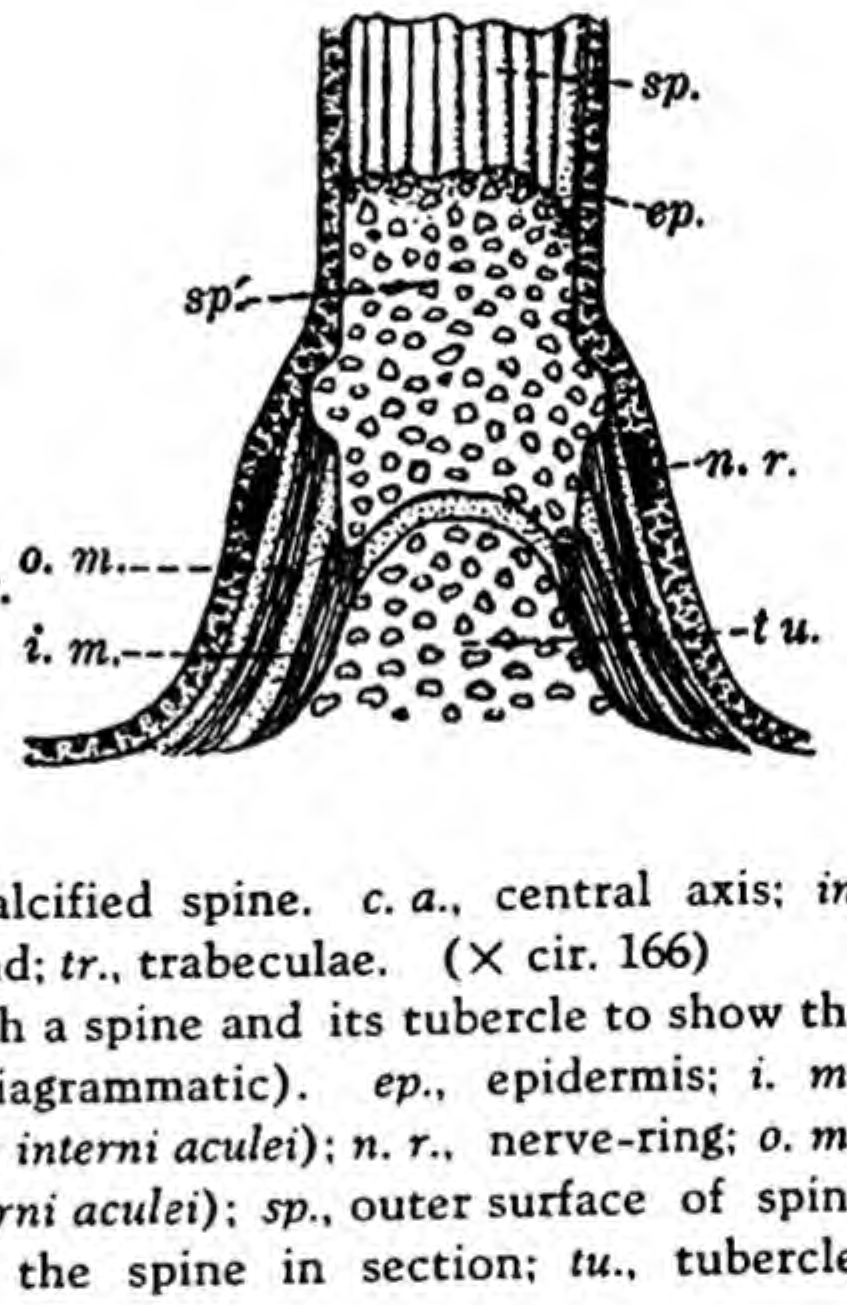


Fig. 2.—A transverse section of a decalcified spine. *c. a.*, central axis; *in. tr. s.*, inter-trabecular spaces; *o. r.*, outer rind; *tr.*, trabeculae. (× cir. 166)

Fig. 3.—A longitudinal section through a spine and its tubercle to show the muscular sheath and nerve-ring (semi-diagrammatic). *ep.*, epidermis; *i. m.*, internal muscular sheath (*musculi motores interni aculei*); *n. r.*, nerve-ring; *o. m.*, outer muscular sheath (*musculi motores externi aculei*); *sp.*, outer surface of spine showing the fluted surface; *sp.*, part of the spine in section; *tu.*, tubercle. (× cir. 150)

Microscopically, each spine consists of a central cellular axis from which a large number of radiating lamellae or trabeculae are given off; all these lamellae meet at their outer ends with their neighbours and together form the cylindrical outer rind of the spine. In a transverse section (fig. 2), the structure resembles a wheel, the central axis corresponding to the hub, the radial processes to the spokes and the outer rind to the felloe of the wheel. The spine is deeply impregnated with calcium carbonate, which is deposited chiefly in the form of radiating pillars. In some Echinoids the ridges on the spines closely correspond in number to the trabeculae radiating out from the central axis, but in *Salmacis* there is no such correlation between the two structures.

The spines are of various sizes: the bigger spines, called the *primary spines*, are surrounded by a large number of smaller ones called the *secondary spines* or *spinules*. Further, the spines immediately surrounding the peristome (fig. 1) are blunt and oar-shaped, and may possibly be used for shovelling mud into the mouth.

Besides the spines, the surface of the urchin is beset with five double rows of delicate and translucent cylindrical structures bearing suckers at their ends: these are the *tube-feet*. Each of these double rows runs along a meridional region of the surface of the body called the *ambulacral area*, corresponding to the ambulacral groove of the starfish. Thus there are five meridionally disposed ambulacral areas and alternating with them there are five *inter-ambulacral areas*, which are devoid of tube-feet. In a living animal the tube-feet attach themselves by their suckers to the substratum or to the sides of the glass-vessel, and so pull the body along in any desired direction. The tube-feet are ciliated except at their tips. They are both sensory and respiratory in function in addition to assisting in locomotion[1].

The forest of spines has an undergrowth of small peculiar structures, the *pedicellariae*, arising from the surface of the integument. The pedicellariae are of four kinds, called the *globiferous*, the *tridentate*, the *triphyllous*, and the *ophicephalous*. Each pedicellaria consists of three blades or jaws mounted on a long

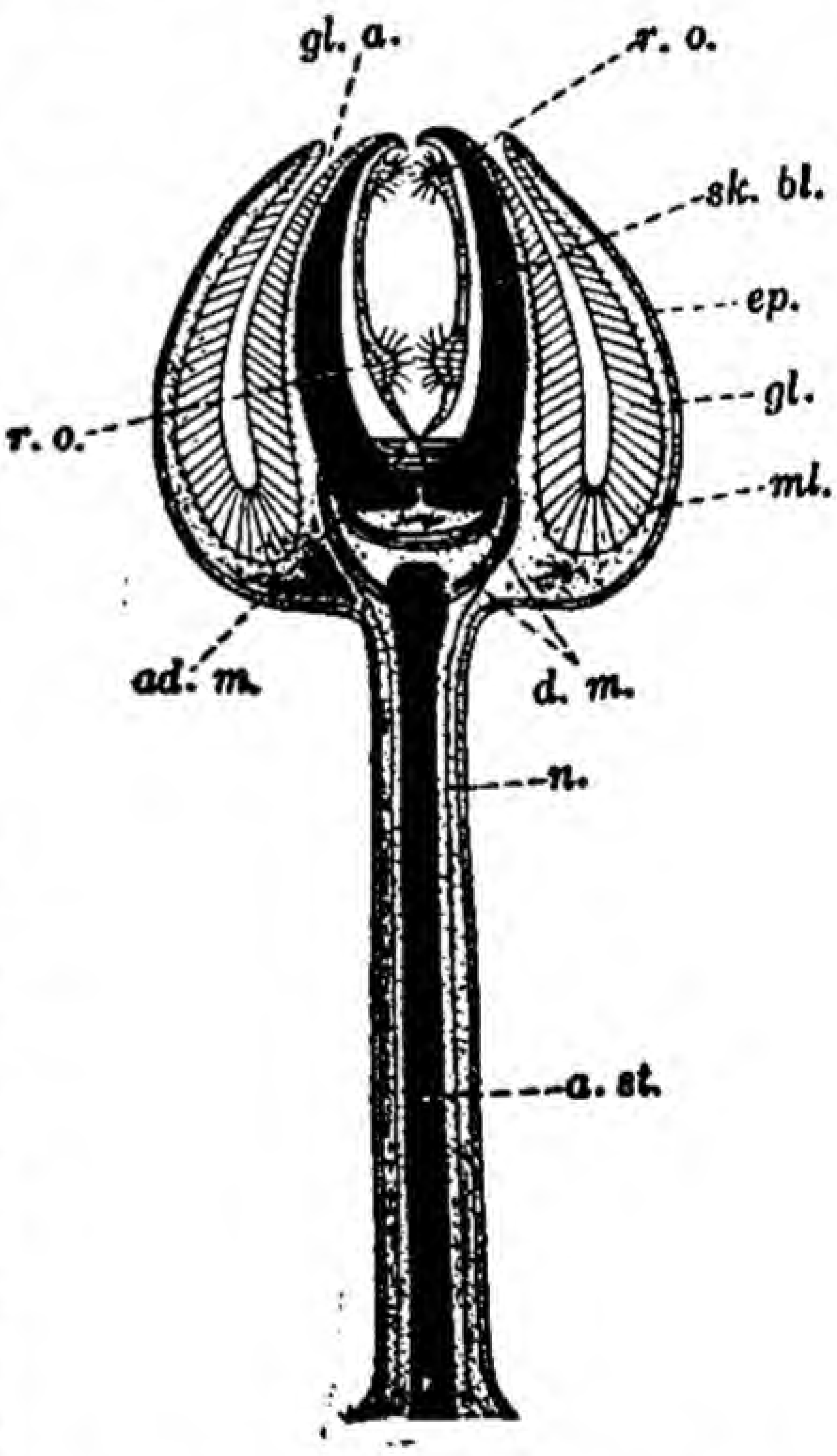


Fig. 4.—Diagram of a gemmiform pedicellaria (modified from Lang). *a. st.*, calcareous axis of the stalk; *ad. m.*, adductor muscle; *d. m.*, divaricator muscles; there are two muscles: the outer muscle between the end of the stalk and the outside of the blades is referred to in the text as a *flexor*, while the inner muscle is called the *divaricator*; *ep.*, epidermis; *gl.*, gland; *gl. a.*, aperture of the gland; *ml.*, muscular layer outside the gland; *n.*, nerve-fibre to the muscle; *r. o.*, receptor organ; *sk. bl.*, calcareous skeletal blade of the jaw.

[1] Further details regarding tube-feet are given in the chapter on the water vascular system.

stalk and a well developed musculature for opening and closing the jaws (fig. 4). The stalk contains a calcareous rod which articulates with a minute tubercle on the test. Like the spinules, the pedicellariae are covered with ciliated epithelium which is modified to form special receptor organs on the inner surface of the blades.

(1) The *globiferous* or *gemmiform* (Lat. *gemma*, a bud) *pedicellariae* are distinguished by the fact that the calcareous supporting rod in the stalk extends to the very base of the blades, each of which carries a pair of bag-like glands on its outer surface (figs. 4, 5 and 6). Each blade is triangular in shape with a pointed curved tooth at its extremity; each gland of a pair leads into a duct which unites with its fellow to form a common duct running along a narrow groove on the inner surface of the tooth and opening to the exterior through a pore at the tip of the tooth. Well developed muscles bring about the contraction of the glands for the discharge of the poisonous secretion.

The blades or jaws are provided with three sets of muscles (fig. 4): (1) the *adductors* which are inserted on the inner surfaces of the blades and close the jaws by their contraction, (2) the *divaricators* which are inserted on the outside of their bases and by their contraction open the jaws, and (3) the *flexors* which are inserted between the end of the stalk and the outside of the blades; they also help in opening the jaws by their contraction.

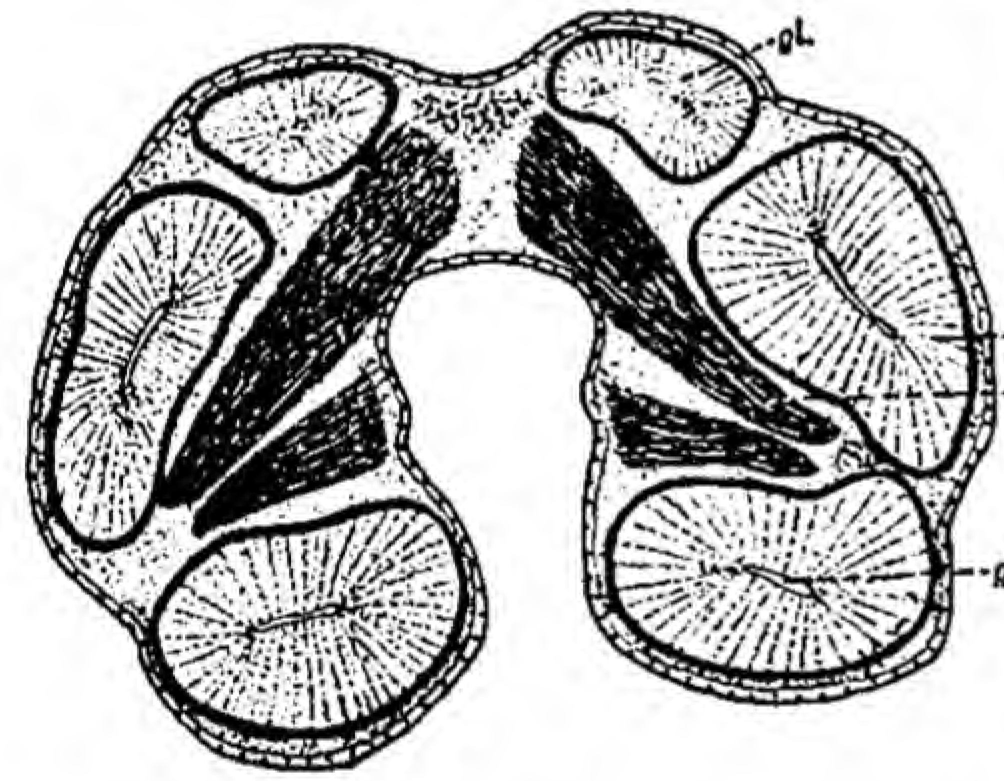
The epithelium on the inner surface of each blade is specially thickened and ciliated at one place to form a receptor organ known as the *neurodermal receptor* (figs. 4 and 6). Apparently, stimuli are received by the receptors and transmitted to the muscles through fine nerves of which there is a rich supply in each pedicellaria (fig. 4).

In *Salmacis bicolor* there are two varieties of globiferous pedicellariae, the large apical variety and the small ordinary variety. The large pedicellariae are confined mostly to the aboral surface of the shell, while the smaller ones are more numerous and are found scattered throughout the surface of the body. The blades of the two types also differ; in the larger apical pedicellariae there is no lateral tooth below the main fang (fig. 8 B), while in the smaller ordinary ones each blade has a lateral tooth in addition to the main fang (fig. 8 A).

(2) The *ophicephalous* (snake-headed) *pedicellariae* (fig. 7 C) are very numerous and are found scattered all over the shell.

The stalk is supported proximally by a calcareous rod extending to about half its length; the distal half, devoid of the rod, contains an elastic band in the axis and is therefore flexible and mobile. The blades are oval and possess several small teeth along their margins. These pedicellariae have neither glands nor neurodermal receptors.

(3) The *tridentate pedicellariae* are rather small in size but are very numerous. The axial supporting rod extends less than half way through the stalk (fig. 7 D), the



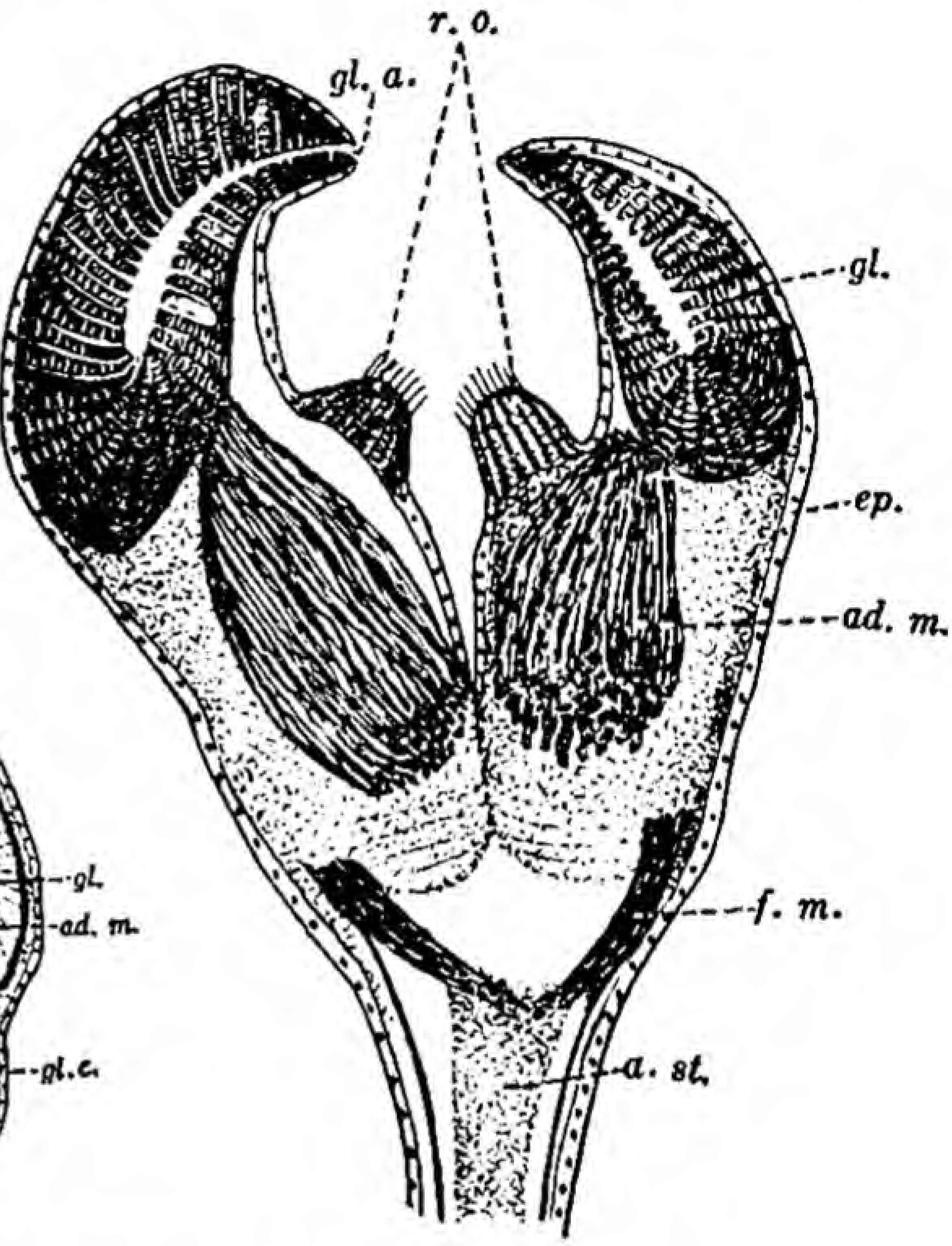


Fig. 5.—A transverse section of a globiferous pedicellaria. *ad. m.*, adductor muscle; *gl.*, gland; *gl. c.*, gland-cavity. (× cir. 285)

Fig. 6.—A longitudinal section of a globiferous pedicellaria. *a. st.*, axis of stalk; *ad. m.*, adductor muscle; *ep.*, epidermis; *f. m.*, flexor muscle; *gl.*, gland; *gl. a.*, aperture of the gland; *r. o.*, receptor organ. (× cir. 315)

blades are elongated and triangular in shape but their lateral margins are concave, so that when a pedicellaria is closed, the three blades meet at their bases and apices, but their lateral margins do not come in contact. The blades carry three to five broad irregular teeth on each side, and at the base there is a well developed meshwork (figs. 8 D and D′).

(4) The *triphyllous* pedicellariae are the smallest in size. The supporting rod extends for about half the distance of the stalk, the distal portion of which contains elastic tissue and is highly flexible (fig. 7 E). The blades have no teeth and are leaf-like and hence the name (fig. 8 E).

The globiferous pedicellariae are absent from the peristome, but the ophicephalous, tridentate, and triphyllous types are found in groups surrounding the buccal tube-feet (fig. 1). It is believed that pedicellariae are really sets of three spines arranged to bite together like pincers.

The pedicellariae act both as organs of defence and offence. For example, when a sea-urchin is inundated with a

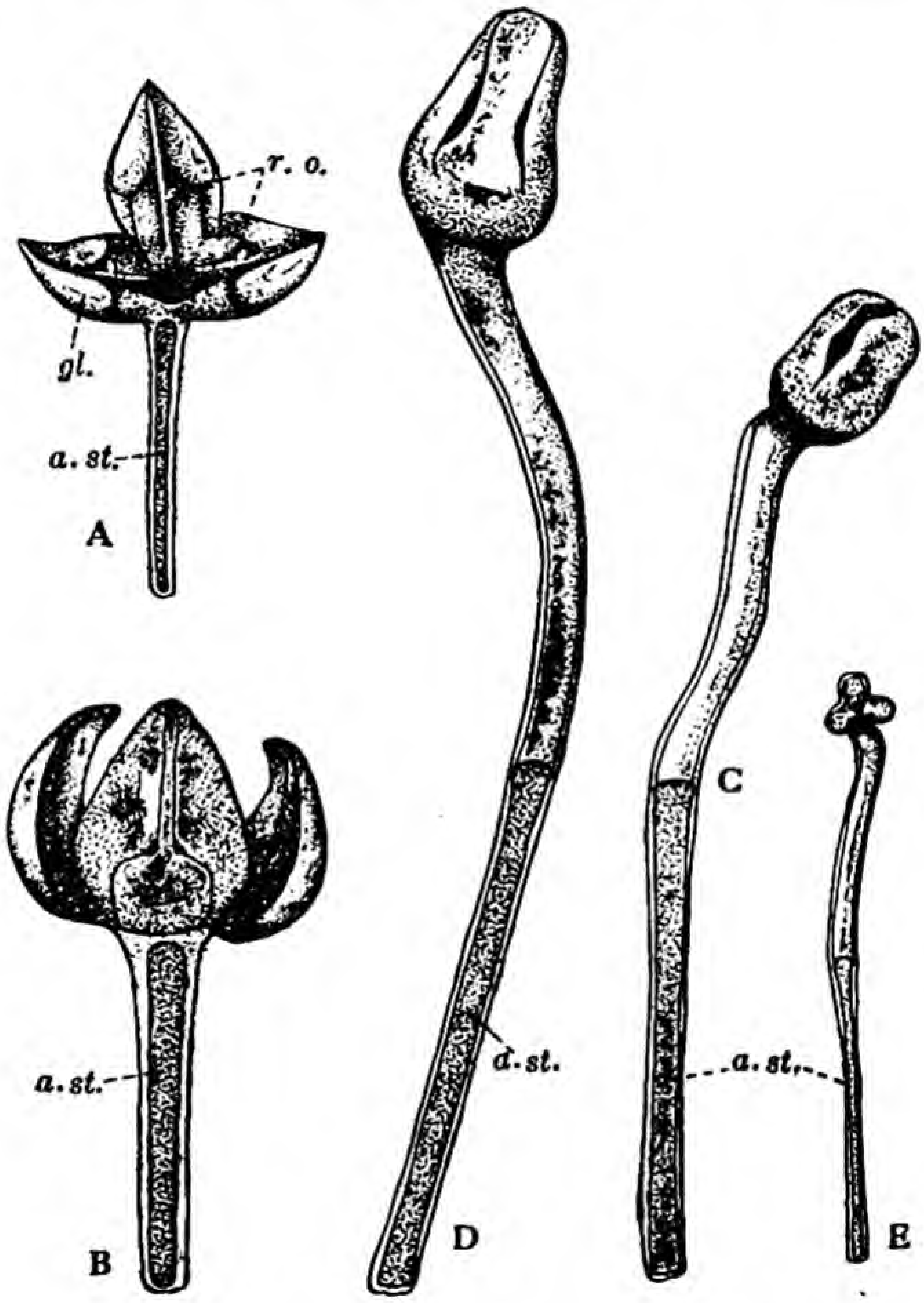


Fig. 7.—Different types of pedicellariae. A. Ordinary globiferous pedicellaria (× cir. 50). B. Apical globiferous pedicellaria (× cir. 32). C. Ophicephalous pedicellaria (× cir. 20). D. Tridentate pedicellaria (× cir. 20). E. Triphyllous pedicellaria (× cir. 20). *a. st.*, calcareous axis of the stalk; *gl.*, gland; *r. o.*, receptor organ.

shower of particles of mud or sand, each particle is gripped by one of the triphyllous pedicellariae which holds it with two blades, whilst the third hammers the particle into dust which is

swept away by the cilia. In this way these pedicellariae help in the removal of dirt and have therefore been called "cleaning pedicellariae". It has been proved that globiferous pedicellariae are able to paralyse small organisms; a single pedicellaria of this type is able to paralyse a frog's heart by its bite because of the poison secreted by its glands. The ophicephalous or bull-dog

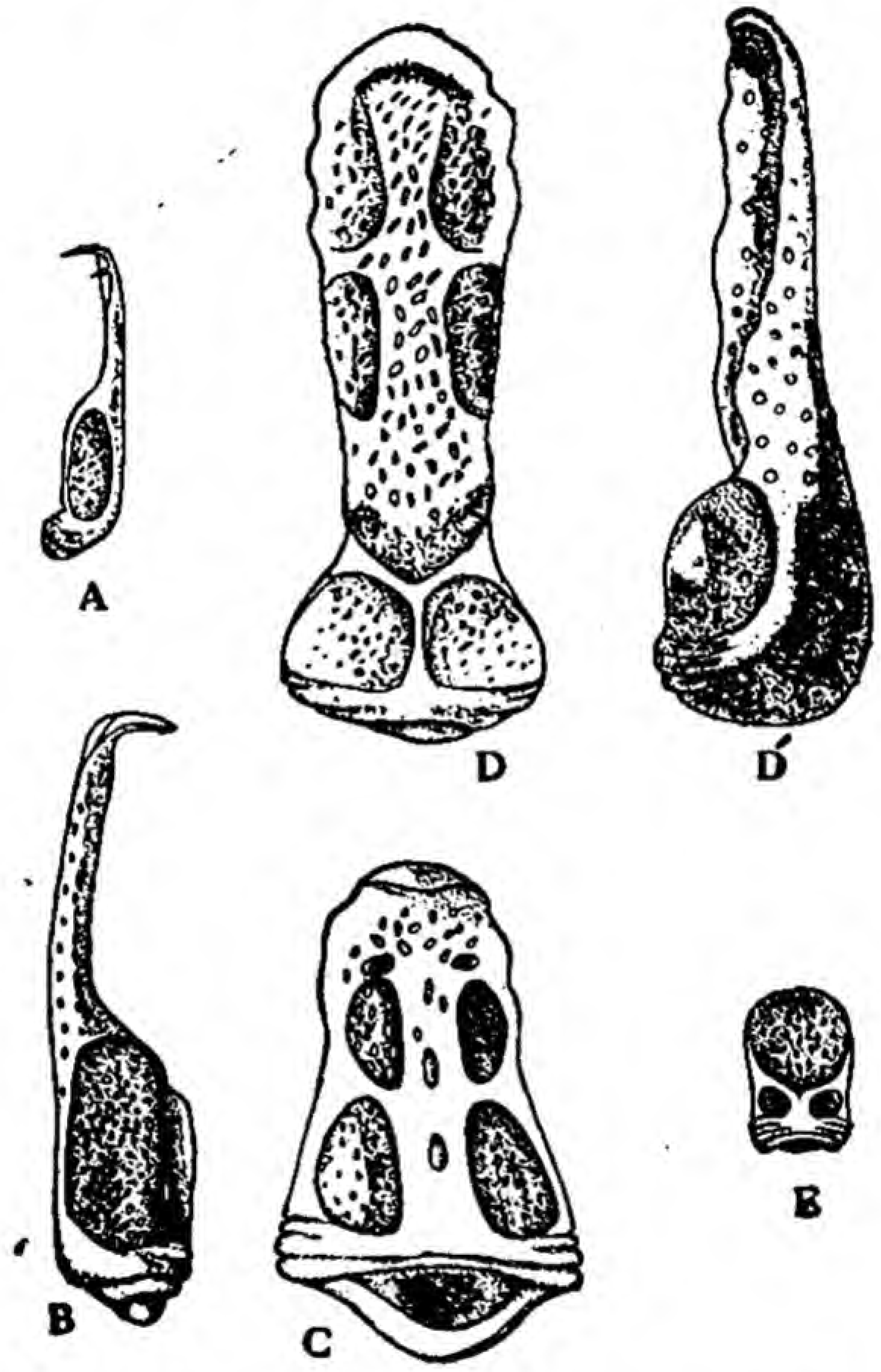


Fig. 8.—Blades of different kinds of pedicellariae. A. Blade of an ordinary globiferous pedicellaria showing a lateral fang. B. Blade of an apical globiferous pedicellaria. C. Blade of an ophicephalous pedicellaria. D and D′. Front and side views of a blade of a tridentate pedicellaria. E. Blade of a triphyllous pedicellaria. (× cir. 86)

pedicellariae grip larger prey such as small worms which may brush against the urchin; they hold fast the prey till the tube-feet take it up and convey it to the mouth. Finally, the tridentate pedicellariae, which are very sensitive, seem to seize small organisms such as the larvae of sponges, coelenterates, and Protozoa, which they hold till their captives die. In this way the

delicate skin of the urchin is always kept clean. Jennings[1], in his work on *Asterias forreri*, has clearly demonstrated that not only small animals like Copepods but also several large crustacea are caught by the pedicellariae. He reproduces, for instance, a photograph of this starfish holding five large specimens of the crab *Hippa analoga*.

"Prouho has described a combat between a sea-urchin and a starfish. When the latter approached, the spines of the sea-urchin diverged widely (strong form of reaction to chemical stimulus), exposing the gemmiform pedicellariae. These at once seized the tube-feet of the enemy and the starfish retreated, wrenching off the heads of these pedicellariae; then the starfish returned to the attack and the same result followed, and this was repeated till all the pedicellariae were wrenched off, when the starfish enwrapped its helpless victim with its stomach[2] ".

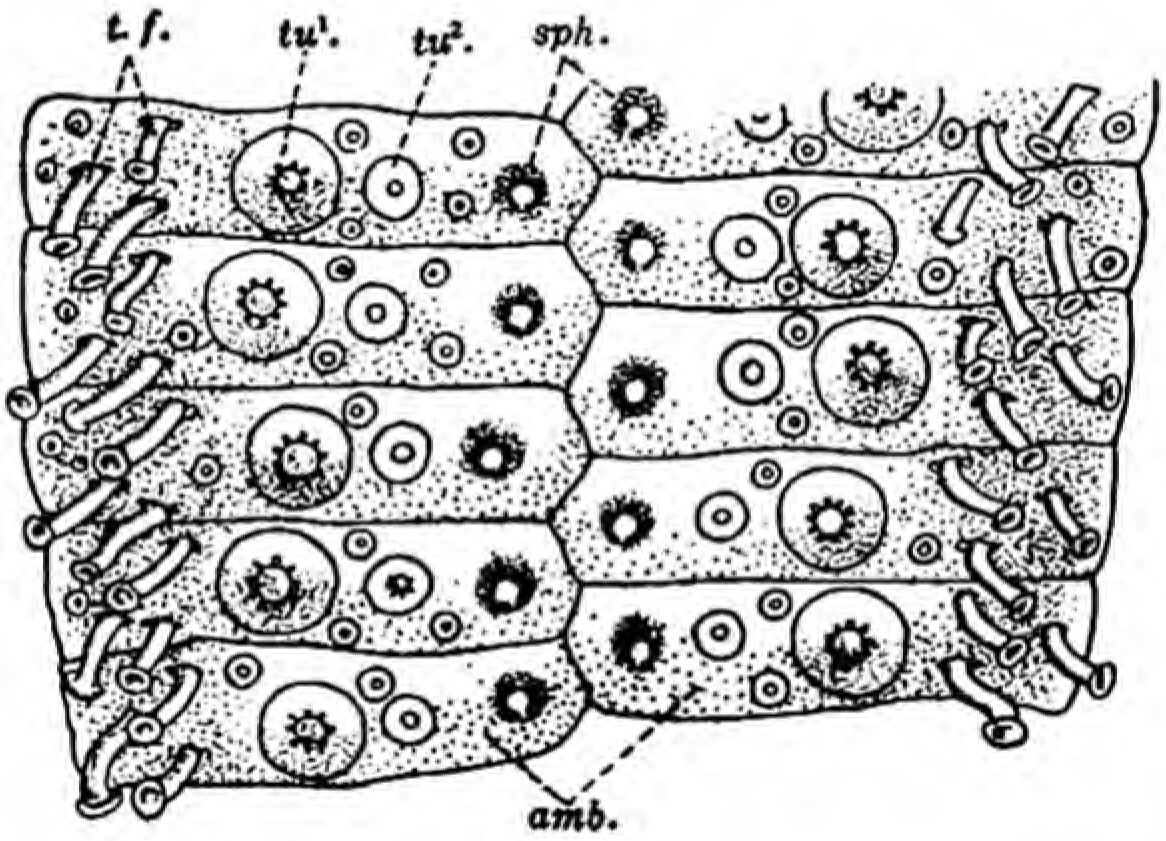


Fig. 9.—Part of an ambulacrum showing the position of the sphaeridia. *amb.*, ambulacral plates; *sph.*, sphaeridia; *t.f.*, tube-feet; *tu1*., primary tubercle; *tu2*., secondary tubercle. (× cir. 7)

Lying amongst the spines and tube-feet, mainly in the radii of the oral surface are minute, glassy, club-shaped structures, covered with cilia and possessing a rich supply of nerves at their bases. These glassy spheres, called the *sphaeridia*, are attached to the ambulacral plates by means of short stalks. In a living urchin the sphaeridia are observed to be in a state of constant movement; they are almost certainly balancing organs.

1 California Publ. Zool. vol. 4, 1907.

2 Quoted from MacBride's article in the Cambridge Natural History, vol. i, pages 509-510.

CHAPTER III

THE SKELETON

On removing the spines and pedicellariae the body is seen to be enclosed in a firm immovable skeleton called the *test*. The test is composed of calcareous dermal plates fitting closely and rigidly against one another by means of sutures. These dermal plates lie beneath the ciliated epidermis but outside the nervous and water-vascular systems, and occur

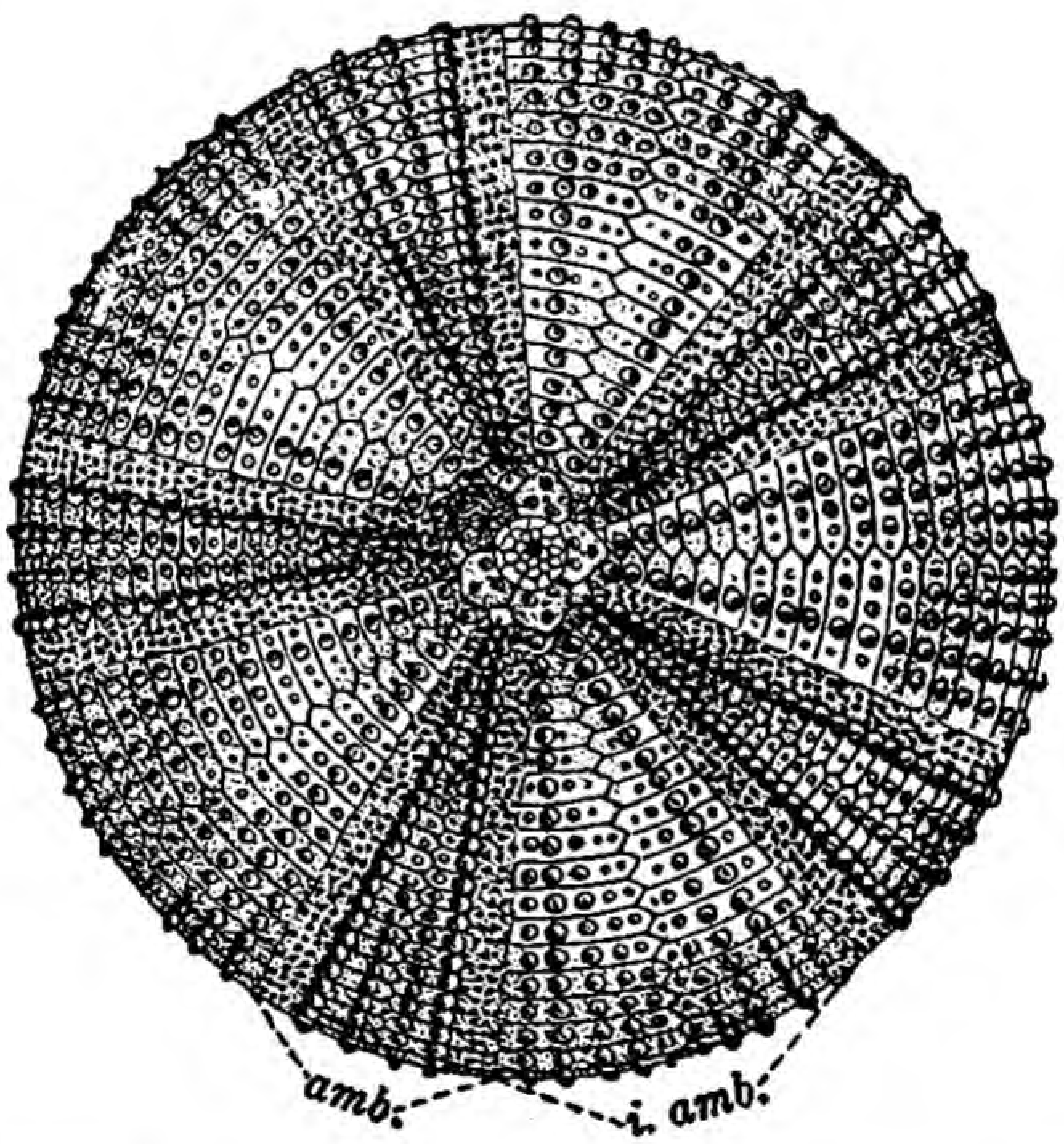


Fig. 10—The ambitus. *amb.*, ambulacrum; *i. amb.*, inter-ambulacrum. (× cir. $1\frac{3}{5}$)

in three groups: (1) the plates of the globular shell or *corona*, (2) the plates of the apical system imbedded in the periproct, and (3) the plates in the peristomial membrane. In addition to these plates there is a complicated framework of calcareous plates and rods which surround the gullet and are together known as the *lantern of Aristotle*.

The *corona* is formed of ten double rows of *coronal plates* arranged meridionally from the outer edge of the peristome to the periproct; five of these double rows are radial in position and form the *ambulacra*, while the other five are inter-radial and form the *inter-ambulacra*. The outline of the corona as viewed from the aboral pole is often called the *ambitus* (fig. 10). The ambulacral double row of plates is easily distinguished in a living specimen by the presence of two rows of tube-feet (fig. 9) running all along its length, one along each margin,

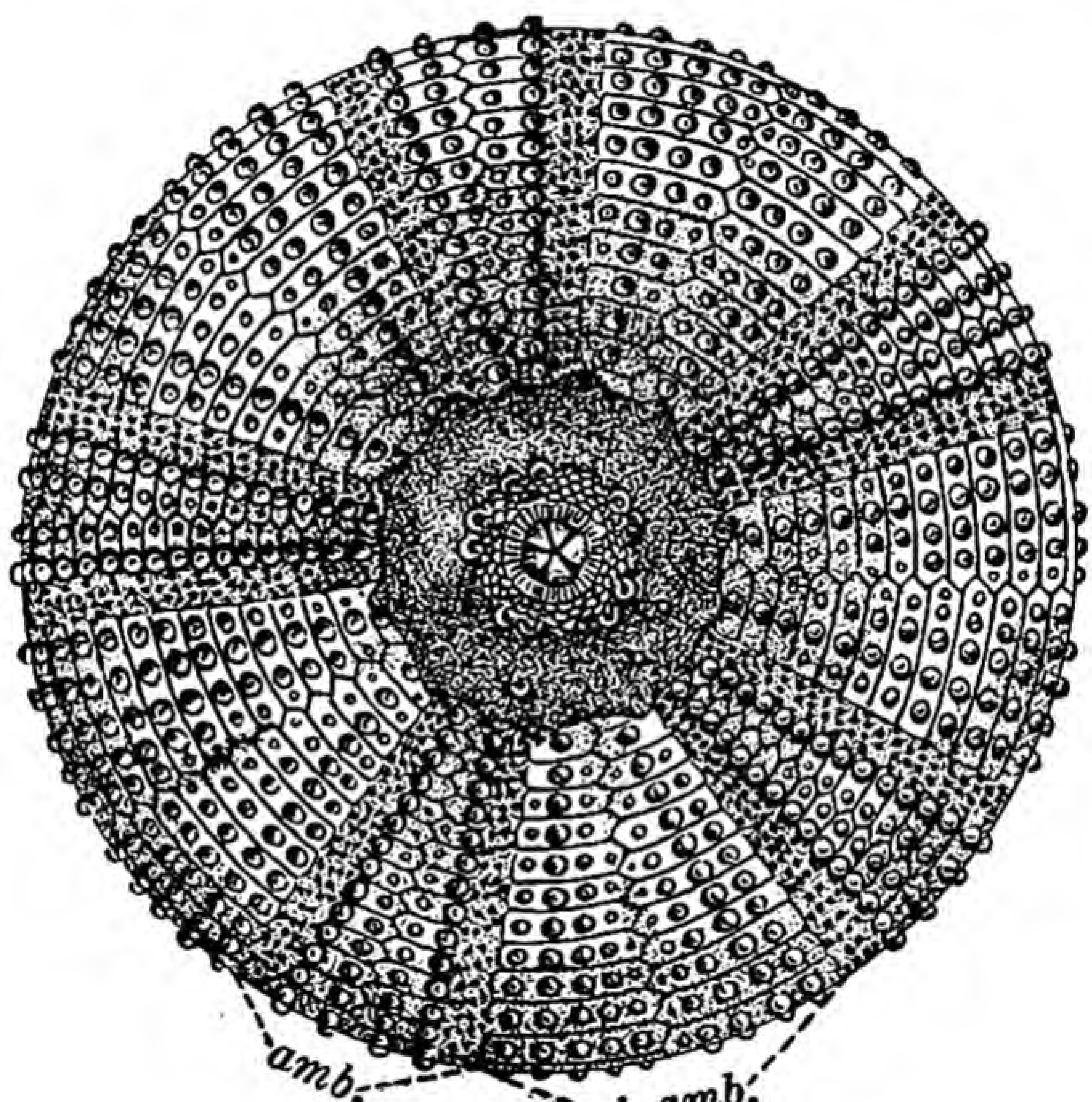


Fig. 11—The corona as seen from the oral pole. *amb.*, ambulacrum; *i., amb.*, inter-ambulacrum. (× cir. $1\frac{3}{5}$)

the tube-feet being absent from the inter-ambulacral plates. On removing the tube-feet, each ambulacral plate (fig. 12) is seen to be pierced by three pairs of openings through which the tube-feet perforate the shell. The line dividing each ambulacral area from the adjoining inter-ambulacral area is more or less straight, but that dividing one row of ambulacral or inter-ambulacral plates from the adjoining row of similar plates is zig-zag (fig. 13). In an animal with a diameter of about 50 mm., there are about *thirty-eight* plates in each of the two rows of an ambulacrum,

while there are only *twenty-nine* in each of the two rows of an inter-ambulacrum. Both kinds of plates are more or less rectangular in shape, but as one of the smaller sides always presents a projection, all the plates may be said to possess five sides. They all carry tubercles or bosses of three sizes on their outer surface, the *primary tubercles* for carrying the largest spines, the *secondary* for carrying medium-sized spines, and the *tertiary* or very minute ones for the articulation of very small spines or pedicellariae.

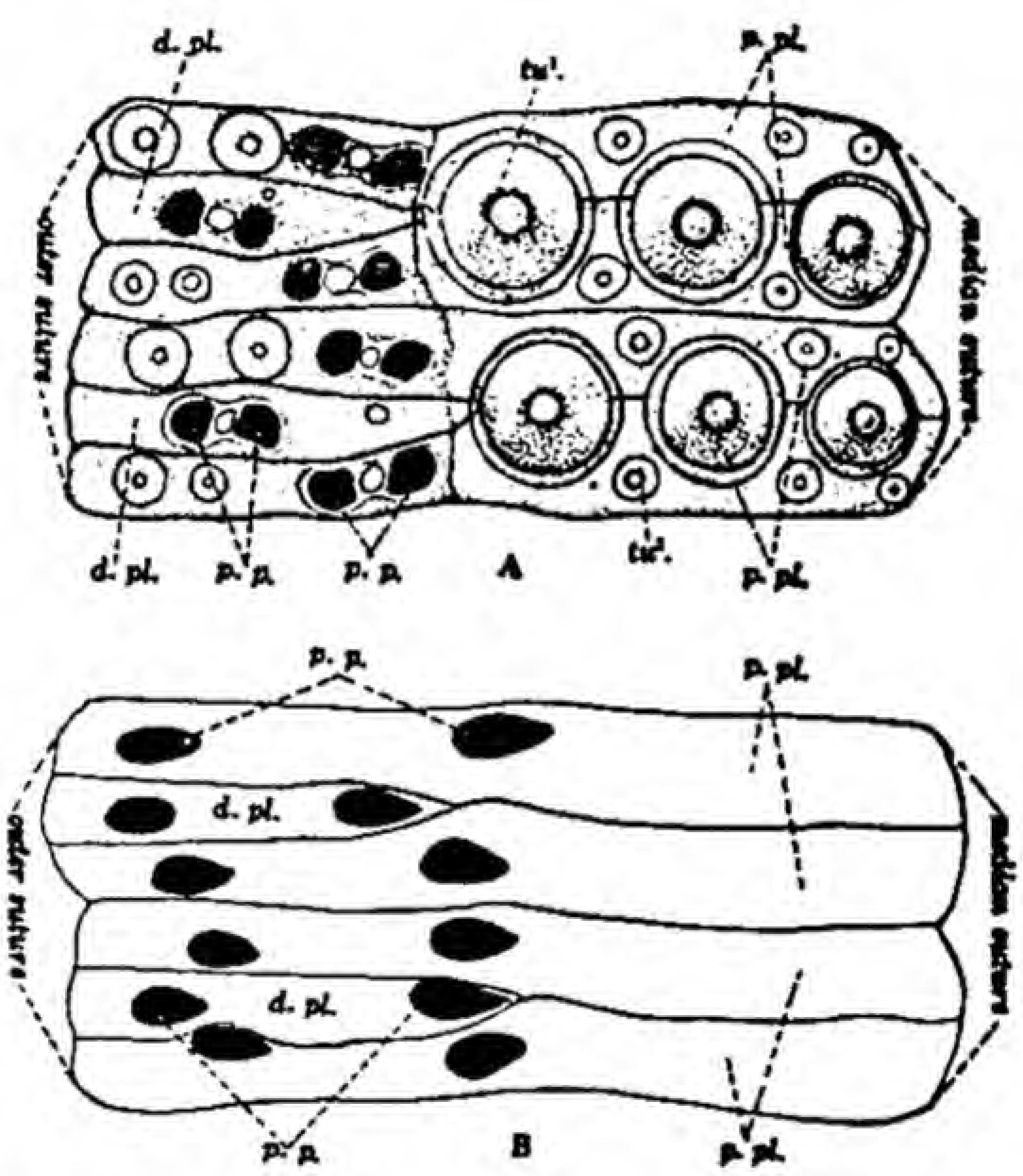


Fig. 12—Two ambulacral plates. A. Outer surface. B. Inner surface. *d. pl.*, demi-plates; *p. pl.*, primary plates; *p. p.*, pore-pair; tu^1., primary tubercle; tu^2., secondary tubercle.

If an ambulacral plate is treated with caustic potash and thoroughly washed, it is seen to be a composite structure made up of three fused plates, the dividing lines between which are clearly visible, especially on the inner surface (fig. 12). The two lateral borders of an ambulacral plate are distinguished as the *outer* and *median sutures*, the outer suture being contiguous to an inter-ambulacral plate, and the median suture forming the boundary between the two ambulacral plates of the same ambulacrum. Of the three component plates, two are large and elongated, while the third is small and triangular in shape; this small component is called a *demi-plate;* it reaches the outer suture but not the median suture. Of the two large plates, either both of them reach both the sutures, in which case they are called *primary plates*, or one is primary and the other *occluded*, as it reaches the median but not the outer suture. In *Salmacis* both plates are primaries. Each of the three component plates bears a *pore-pair* or *double pore*, so that each ambulacral plate is pierced by three pairs of openings

through which the tube-feet perforate the shell. Plates with three pairs or a lesser number of openings are described as *oligoporous* (e.g. in *Salmacis)* as distinguished from *polyporous* plates (e. g. in *Strongylocentrotus*) in which more than three pairs of openings are found on each ambulacral plate.

The inter-ambulacral plates are larger in size than the ambulacral; they bear no pores, nor are they composite in character (fig. 13). The number of tubercles or bosses for the articulation of spines and pedicellariae varies within wide limits, but there are never less than two primary tubercles on each inter-ambulacral plate at the ambitus. Fig. 15 shows the two adjoining surfaces, at a suture, of an ambulacral and an inter-ambulacral plate, showing the characteristic knobs on the

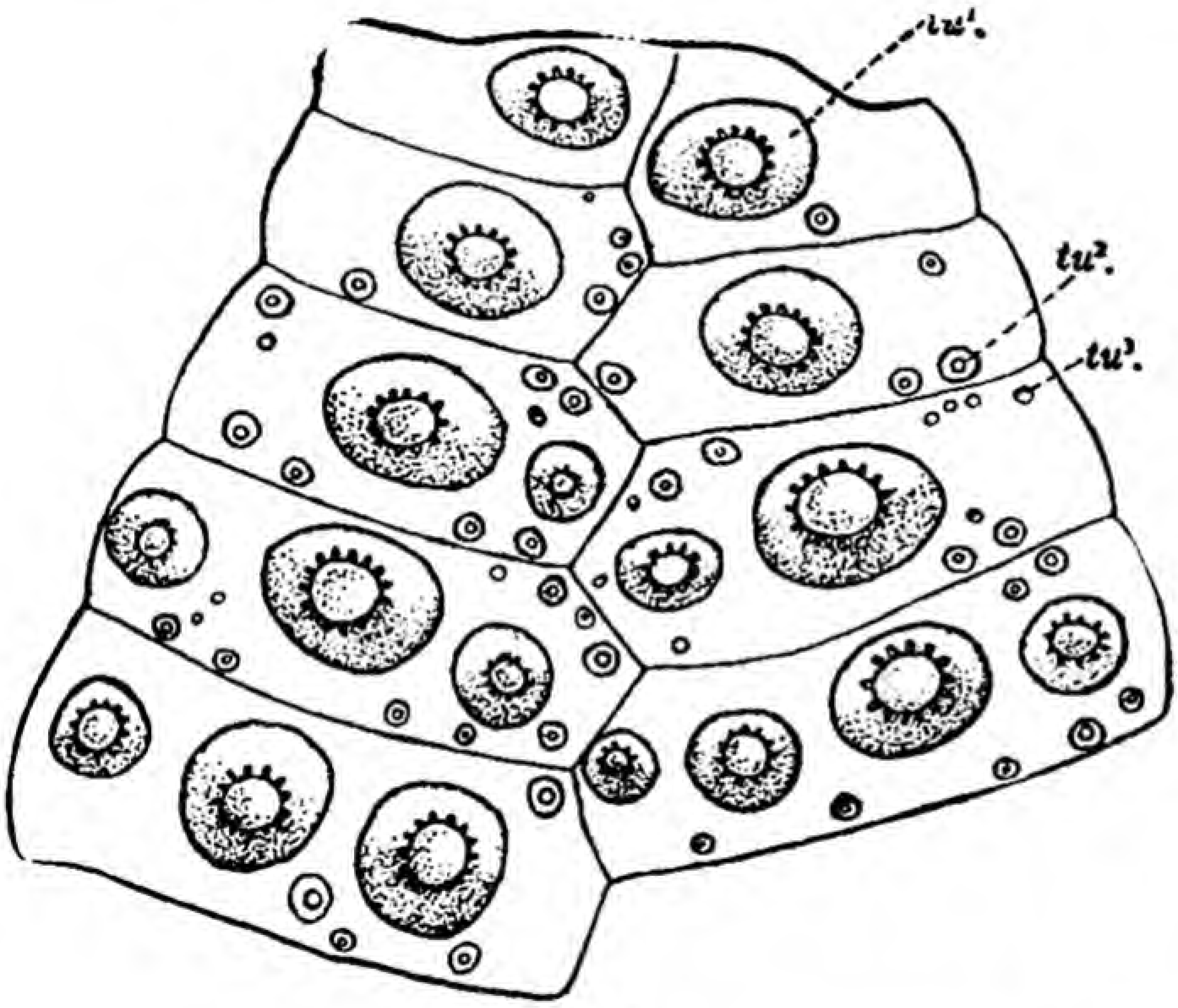


Fig. 13

Fig. 14

Fig. 13—Two rows of inter-ambulacral plates. tu^1 ,. tu^2 ,. tu^3 ,. primary, secondary, and tertiary tubercles. (semi-diagrammatic)

Fig. 14 Bihamate spicules.

ambulacral and pits on the inter-ambulacral surface. These knobs and pits form a distinguishing feature of the urchins belonging to the family Temnopleuridae (Page 6).

The peristomial membrane surrounding the mouth contains small irregular fenestrated plates imbedded in it; of these, five pairs are large and are found opposite the ambulacral areas; these are called the *buccal plates.* C-shaped or bihamate spicules (fig. 14) are also quite common in the peristomial membrane These plates and spicules constitute the *peristomial skeleton.*

In the leathery periproct at the aboral pole are imbedded a number of scattered plates with the anus placed amongst them slightly excentrically (fig 16). Surrounding the periproct there are ten plates, five lying in line with the ambulacral and five in line with the inter-ambulacral areas, the latter being much larger than the former. The smaller plates situated at the ends of the ambulacral zones are called the *oculars*, while the larger plates situated at the ends of the inter-ambulacral areas are called the *genitals* or *basals*. The genitals are so called because each of them is pierced by a well-defined genital pore through which opens the duct of one of the five genital organs. Though the two kinds of plates alternate, it is the genitals that actually form a ring round the periproct, the oculars being shut out from the outer edge of

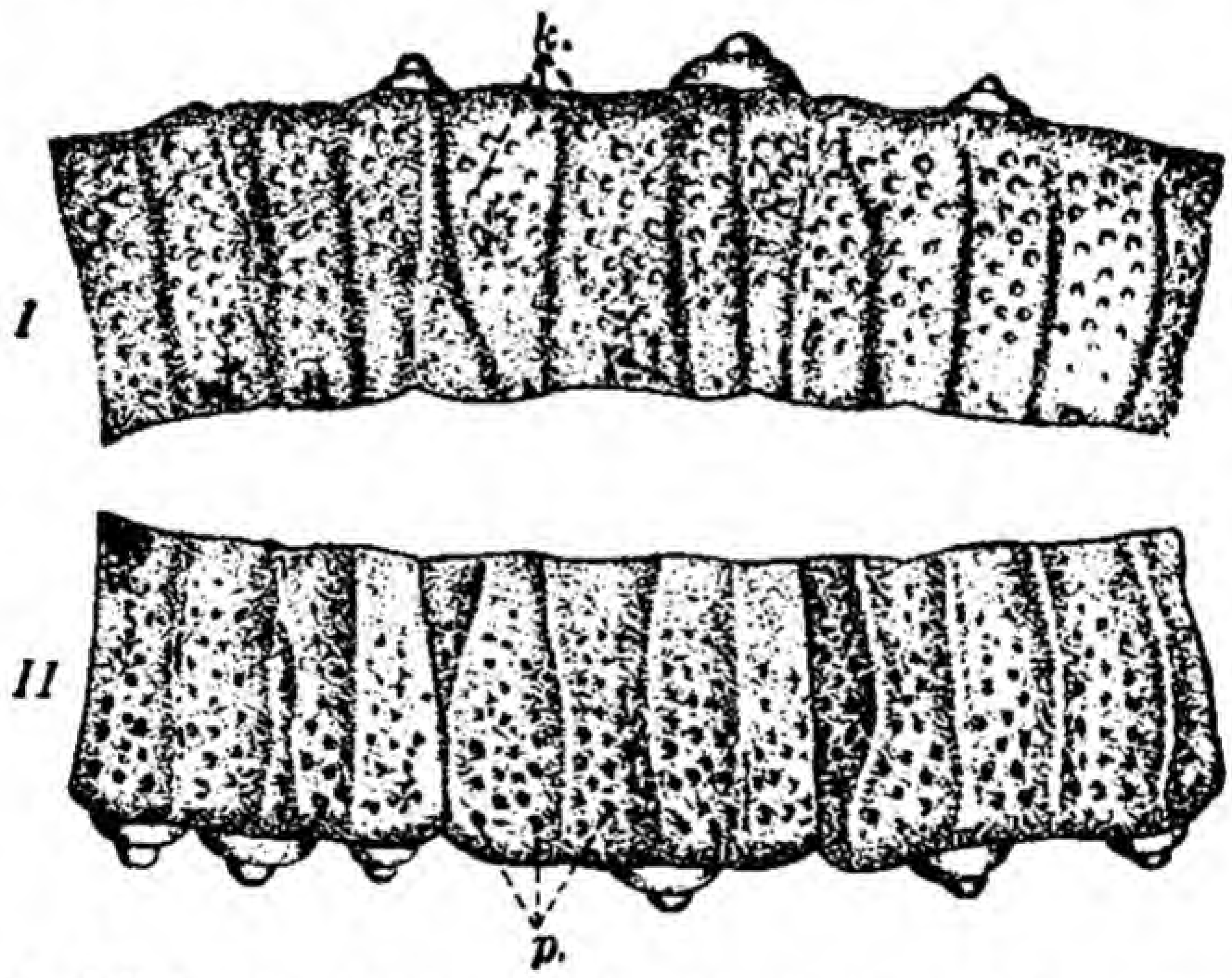


Fig. 15—Adjoining surfaces of (*I*) ambulacral, and (*II*) inter-ambulacra plates at a suture. *k.*, knobs; *p.*, pits.

the periproct. Both the oculars and genitals carry tubercles for the spines. One of the genitals is thicker and slightly larger than the others; it is called the *madreporite*; examination with a lens reveals its pitted appearance, while sections show that it is pierced by numerous minute canals which open below into a space called the *madreporitic ampulla*, from which the stone-canal takes its origin (fig. 27). These pore-canals are separate from one another and are lined by a ciliated epithelium. The ocular and genital plates and the scattered plates imbedded in the periproct constitute the *apical skeletal system* (fig. 16).

In describing the plates of the apical skeletal system a certain enumeration of radii is usually adopted. It is based on what is known as the *Loven's law*

represented in fig. 16. The radius which lies to the left of the madreporite is known as the anterior radius (III), while the two radii which are directed obliquely backwards are known as the posterior radii (V and I). On morphological grounds it has become customary to call the right posterior radius as Radius I, and the rest R II, R III, R IV, and R V in the anti-clockwise direction. The two radii (V and I), one on either side of the posterior inter-radius, constitute the *bivium*, and the remaining three (II, III, and IV) form the *trivium*.

In the centre of the peristome (fig. 11) lies the mouth through which project five white teeth which are keeled. The mouth leads into the pharynx which is surrounded by the masticatory apparatus

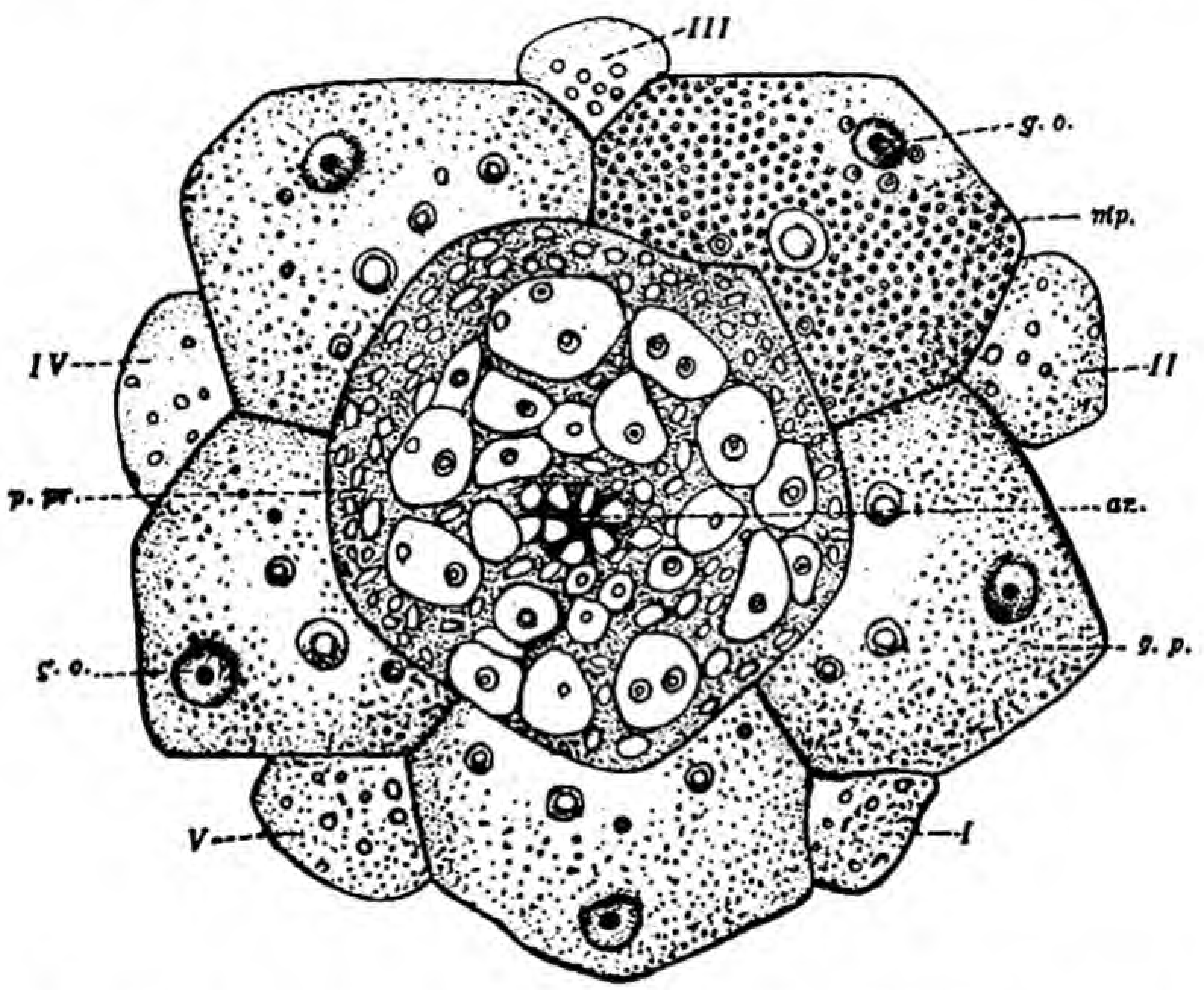


Fig. 16—The apical skeletal system. *an.*, anus; *g. o.*, genital opening; *g. p.*, genital or basal plate; *p. pr.*, periproct; *I, II, III, IV* and *V*, first, second, third, fourth and fifth radii (ocular plates) according to Loven's law; *III* leads to the anterior radius, while *V* and *I* point to the posterior radii.

called the *Aristotle's lantern* (figs. 17 and 18). It consists of: (1) five pyramids, (2) five radial teeth, (3) five epiphyses, (4) five rotulae, and (5) five compasses, twenty-five pieces in all. All these ossicles and the muscles attached to them are inserted in the outer walls of five sac-like cavities which are collectively termed the "lantern coelom" (Page 32).

The *pyramids* or *alveoli* are inter-radial and vertical in position; each alveolus or "jaw" is made up of two halves which are united along the greater part of their length through a longitudinal

suture but diverge from each other above so as to leave a triangular space between them (fig. 17A). The outer lateral surface of each half-alveolus (fig. 17C) presents a series of transverse ridges and grooves for the attachment of masticatory muscles. Each one of the five *teeth* is long and curved and lies closely attached and firmly fixed to the middle of the inner surface of an alveolus; the upper end of each tooth projects above and pushes out the roof of the lantern-coelom, while the inner surface of each tooth presents a strongly marked longitudinal ridge. The five *epiphyses* are short curved plates connecting the upper ends of the two halves of each alveolus. The *rotulae* are short rods lying radially between the upper ends of the alveoli; they look like the spokes of a wheel and lie between

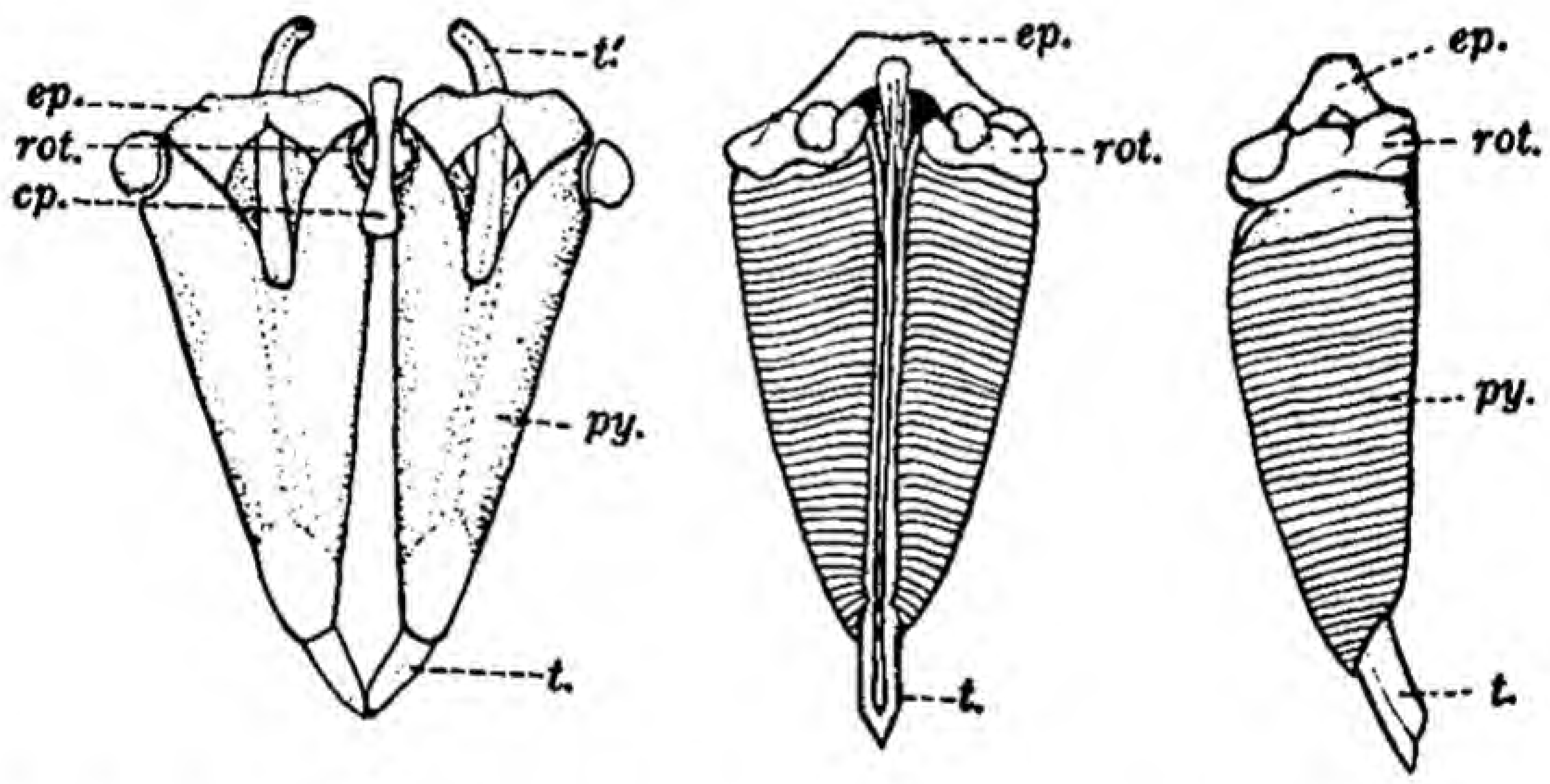


Fig. 17—Lantern of Aristotle. A. External view of two alveoli. B. Internal view of an alveolus. C. Side-view of an alveolus. *cp.*, compass; *ep.*, epiphysis; *py.*, pyramid; *rot.*, rotula; *t.*, lower end of tooth; *t'.*, upper end of tooth.

the upper ends of the adjoining alveoli. Besides these twenty pieces, there are five slender rods lying above and parallel to the rotulae and together forming the so-called "compasses". The compasses lie loosely in the roof of the lantern coelom.

Encircling the Aristotle's lantern and arising from the inner surface of the test there is a circular vertical ridge called the *perignathic girdle*, made up of five arches called the *auricles.* Each auricle (fig. 18) is composed of two halves united by means of a suture, each half of an auricle being an internal projection from an inter-ambulacral plate arising close to the edge of the peristome. The two adjacent halves of an auricle meet in each ambulacral area and form an arched bridge beneath which pass the radial water-vascular canal, the perihaemal canal, the radial blood-strand,

and the radial nerve-cord of that ambulacrum. The auricles are to be compared to the ambulacral ossicles of the starfish.

The lantern is worked by four groups of muscles called the *adductor*, the *divaricator*, the *radial*, and the *masticatory* muscles (fig. 18). These muscles occupy the greater part of the inside of the lantern and also surround it. There are five sets of *masticatory muscles*, each extending between the adjacent pyramids and inserted on their opposing grooved surfaces; the contraction of these muscles draws the five pyramids closer together. Five

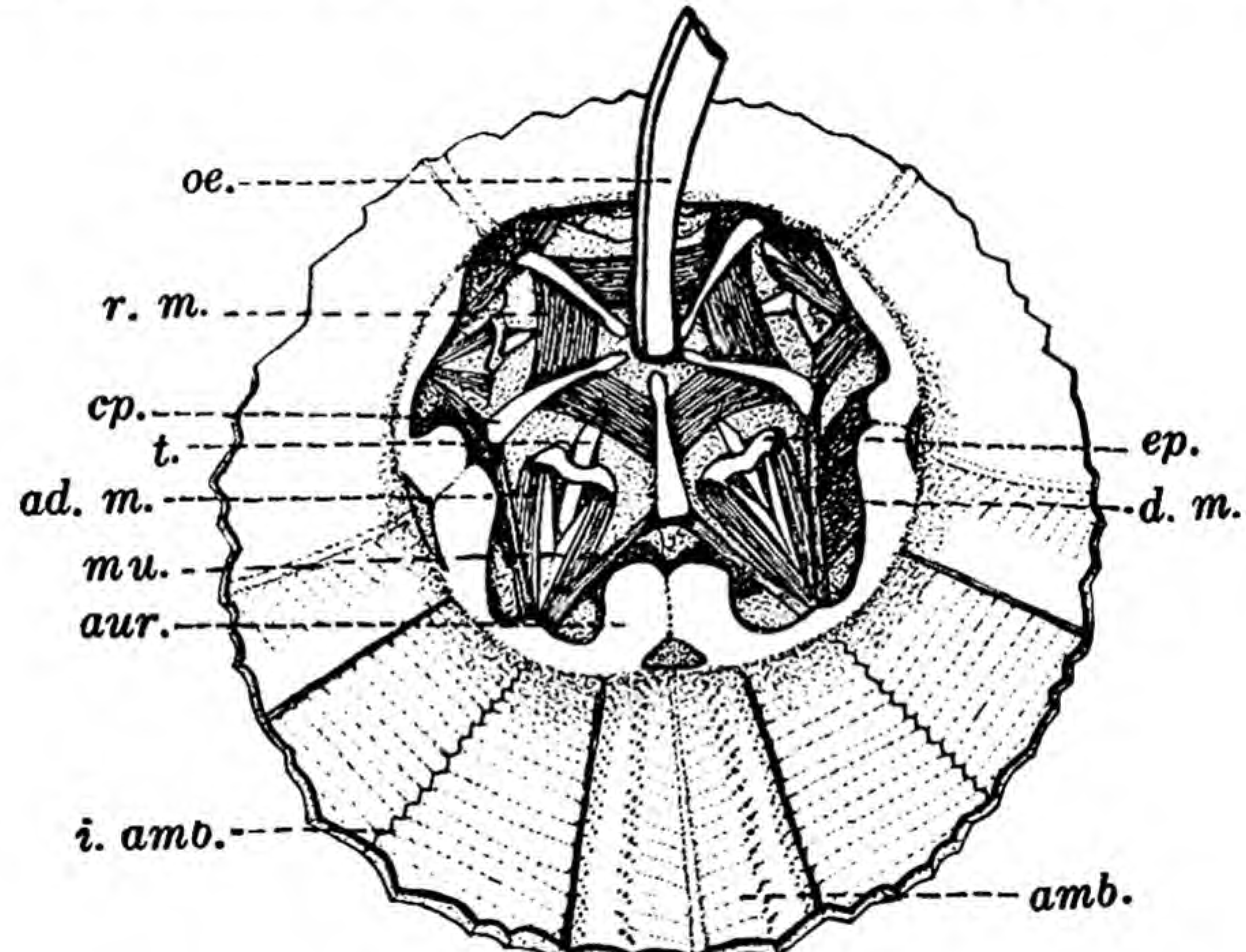


Fig. 18—The lantern apparatus and its muscles. *ad.m.*, adductor muscle; *amb.*, ambulacrum; *aur.*, an auricle of the perignathic girdle; *cp.*, a radius or compass; *d.m.*, divaricator muscle; *e.p.*, epiphysis; *i. amb.*, inter-ambulacrum; *mu.*, depressor muscle of the radii or compasses; *oe.*, oesophagus; *r. m.*, radial muscle; *t.*, upper end of a tooth. (× cir. 3)

pairs of *adductor* (*protractor*) *muscles* are attached, on the one hand, to the low ridges of the perignathic girdle between the adjacent auricles, and are inserted, on the other, on the upper ends of the pyramids; the contraction of these muscles results in pushing the whole jaw-apparatus downward and bringing together and exposing the five teeth; the origin of these muscles is inter-radial, while their insertion is radial. The *divaricators* are short but powerful radial muscles which are attached at their outer

ends to the inner surfaces of the two halves of the auricles, and at their inner ends to the alveolar halves nearest to them; these muscles counteract the action of the adductors, and their contraction pulls the jaw apparatus upwards and makes the tips of the teeth fly apart.

The *radial* muscles are best seen in a top view of the lantern. These five constrictor muscles together form a pentagonal ring connecting the radial rods or the compasses (fig. 18). As a result of their contraction the radial rods become approximated together and project upwards like the ribs of an umbrella thereby raising the roof of the lantern-coelom into the general coelom. The dermal branchiae (Page 8) are outgrowths of the lantern-coelom and consequently the fluid in the lantern-coelom is in communication with that of the gills. When the roof of the lantern-coelom is raised, the fluid is drawn out of the gills into the lantern-coelom and the gills collapse. The *depressor muscles* are five pairs of slender cord-like muscles, each pair being attached internally to the forked outer end of each radius and inserted at their outer ends separately in the centre of two adjacent inter-radii; these muscles pull down and flatten out the radial 'tent', thus expelling the fluid in the lantern-coelom back into the gills which consequently become distended.

Every time the gills expand, they absorb oxygen from the seawater; but when they collapse, their fluid goes into the lantern-coelom which in turn becomes distended; oxygen diffuses from the lantern-coelom into the general coelomic cavity and thus the function of respiration is carried on by the gills and the lantern-coelom with the help of the radial and depressor muscles.

CHAPTER IV

THE ALIMENTARY CANAL

The alimentary canal begins with the *mouth* through which project the five pointed teeth. The mouth leads into the *pharynx* (*stomodaeum*) which passes through the middle of the Aristotle's lantern and emerges into the general coelom as the *oesophagus* (fig. 18). The oesophagus runs vertically upwards as a narrow tube and very nearly reaches the aboral pole, where

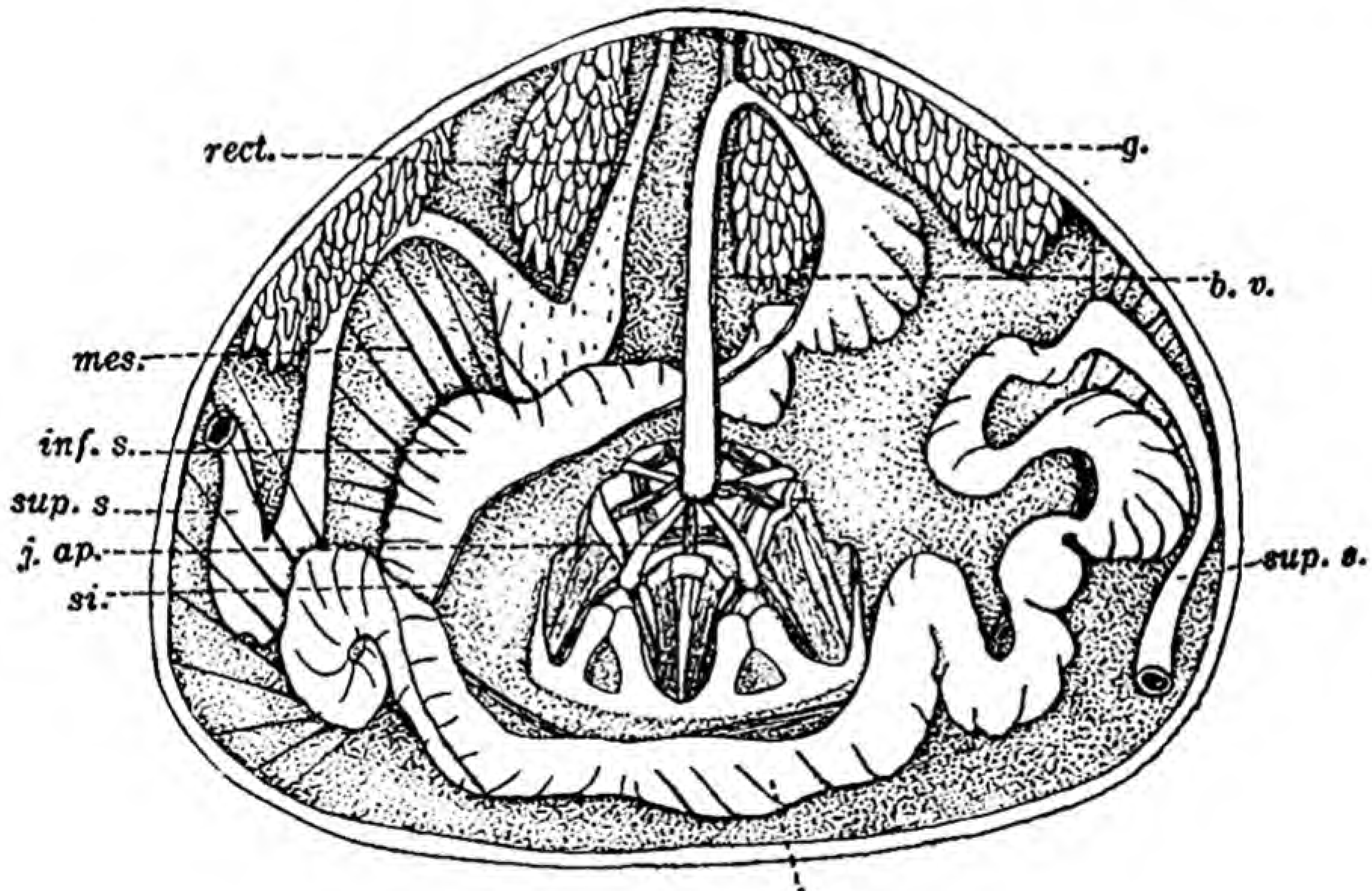


Fig. 19—A diagram showing the disposition of the internal structures *b. v.*, blood-vessel; *g.*, gonad; *inf. s.*, stomach or inferior spiral; *j.ap.*, jaw-apparatus (Aristotle's lantern); *mes.*, mesenterial strands; *si.*, siphon; *sup.s.*, intestine or superior spiral.

it is supported by a suspensory ligament from the plates of the periproct; from this point the oesophagus passes into the *stomach* or *inferior spiral* which bends sharply along the madreporitic interradius and runs obliquely downwards as a flattened bag-like canal almost reaching the oral surface of the test; here it is twisted on itself into a small loop and then runs anti-clockwise as viewed from the aboral pole and makes almost a complete horizontal circle

round the inside of the animal (fig. 19). The stomach is closely pressed against the test and is supported by mesenterial strands from the outer coelomic wall; it is thrown into flattened festoon-like lobes in each radius. On making a "round" and reaching the madreporitic inter-radius again, the stomach turns back on itself and passes into the *intestine* or *superior spiral*, which is also a flattened tube and runs parallel to the stomach round the circumference of the animal in the opposite (clockwise) direction. The superior spiral or intestine continues into the *rectum* which ascends vertically upwards to open to the exterior through the anus. Opening into the inferior spiral (stomach) at its commence-

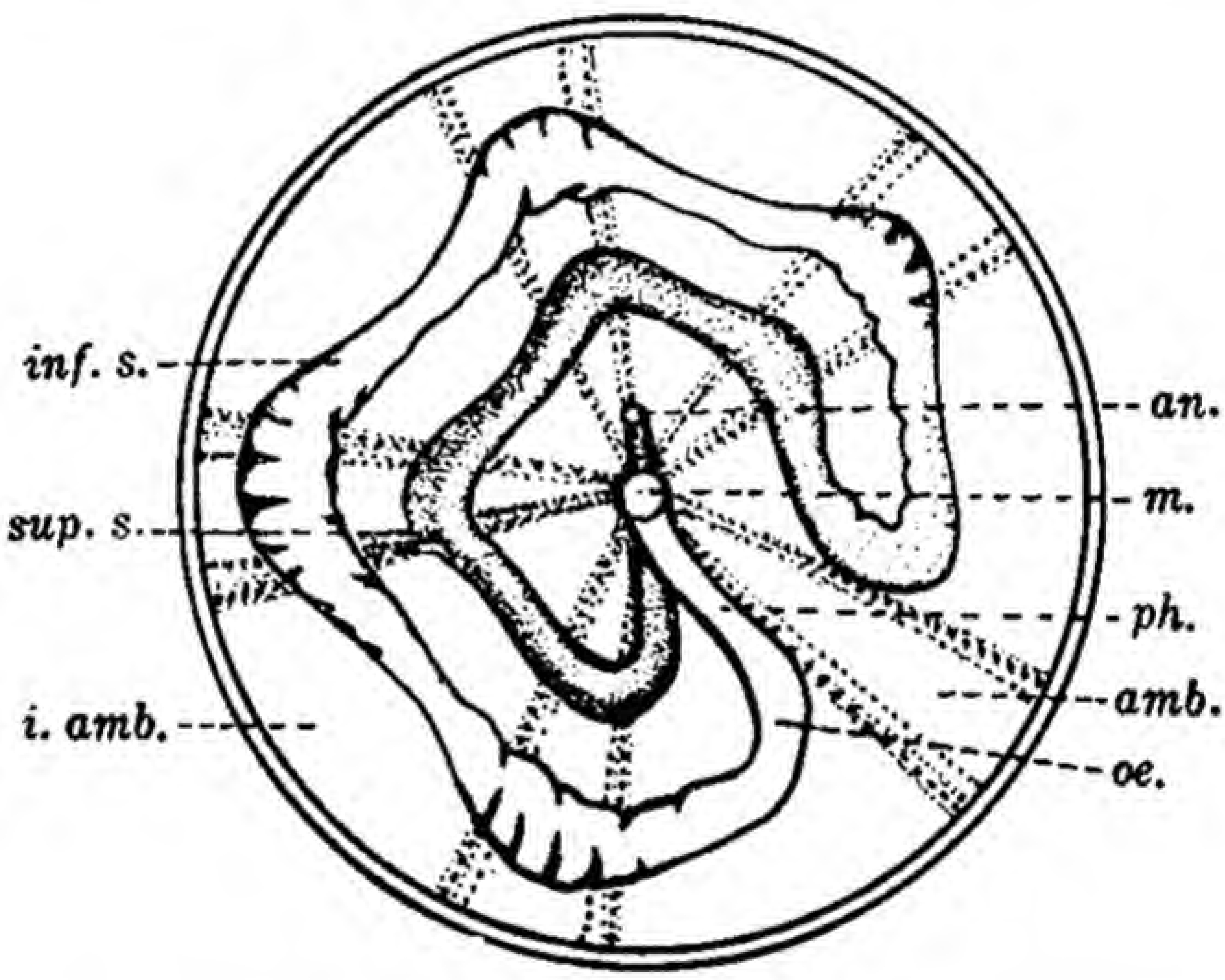


Fig. 20—A diagram showing the course of the alimentary canal, *amb.*, ambulacrum; *an.*, anus; *i. amb.*, inter-ambulacrum; *inf. s.*, inferior spiral; *m.*, mouth; *oe.*, oesophagus; *ph.*, pharynx; *sup. s.*, superior spiral.

ment, there is a narrow cylindrical tube called the *siphon*; the siphon runs along the inferior spiral and opens again into it a little distance before it passes into the superior spiral. As it opens into the stomach at both ends, the siphon is believed to be a groove of the stomach which has been constricted off all along its length. The siphon is lined with cilia (fig. 21) and it is believed that it keeps up a stream of fresh seawater that passes through the gut for purposes of respiration. In some forms like *Dorocidaris papillata* the siphon is absent.

The inferior spiral or the stomach differs from the superior spiral in being highly sacculated and also in having a reddish

colour. The rectum has smooth external walls and is attached at its distal end to the inner surface of the test by means of a large number of muscular strands.

The pharynx is five-rayed in section and has a narrow lumen. Projecting into it are five triangular cushions of long fusiform cells alternating with simple fold-like structures. In *Dorocidaris papillata* Prouho speaks of a large number of *calciferous glands* lying amongst the elongated cells of the pharynx. He distinguishes two types of cells in these glands, one with a granular cytoplasm, and the other with a homogeneous cytoplasm, but both secreting mucus. The calciferous glands, according to him

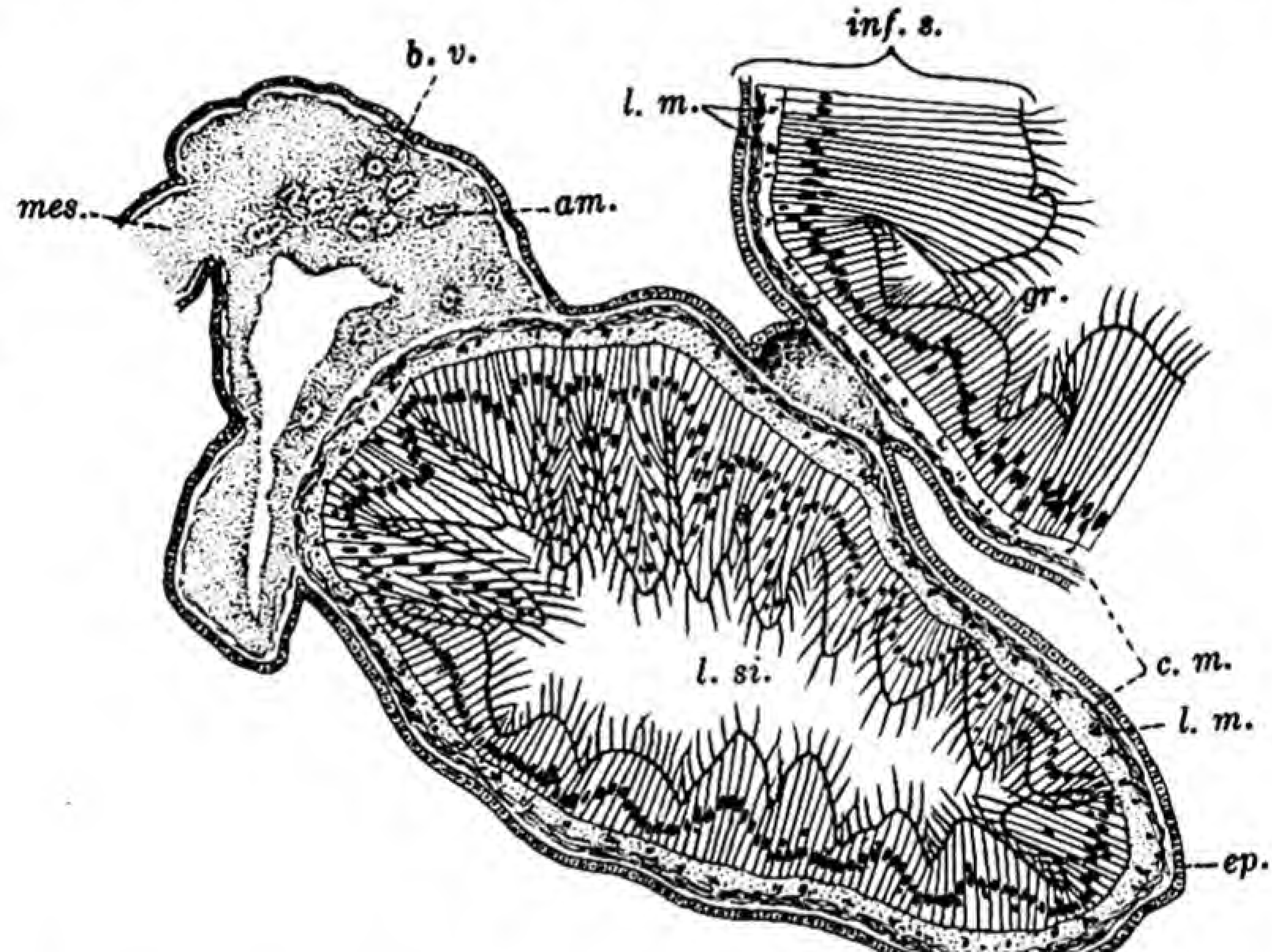


Fig. 21—A transverse section passing through the intestine and siphon to show their similarity of structure. *am.*, amoebocytes; *b. v.*, blood-vessel; *c. m.*, circular muscle layer; *gr.*, intestinal groove; *inf.s.*, inferior spiral; *l.m.*, longitudinal muscle layer; *l.si.*, lumen of siphon. (× cir. 50).

are therefore merely mucus-secreting glands. The wall of the pharynx consists of an outer ciliated layer of coelomic epithelium, a layer of well-developed connective tissue, a layer of muscle-fibres, a layer of fusiform cells which are often ciliated, and lastly, a thin internal cuticular layer.

The stomach and the intestine (figs. 21, 22 and 23) consist of the coelomic epithelium, a thin layer of circular muscles, a layer of longitudinal muscles, a layer of connective tissue, a layer of fusiform cells lining the folds projecting into the lumen, and

finally a thin cuticular membrane. Among the fusiform cells of the folds projecting into the lumen are seen a large number of gland-cells which are more numerous in the inferior spiral than in the superior spiral. The siphon (fig. 21) accompanying the stomach has the same structure as the stomach itself. The mesenteries supporting the coils have an epithelial, a muscular, and a connective tissue layer.

The rectum (fig. 24) resembles the intestine in its histological characters but its walls have more of connective tissue and thicker muscular layers, and the internal folds are more numerous. Bihamate spicules (Page 20) are of common occurrence in the connective tissue layer of the entire alimentary

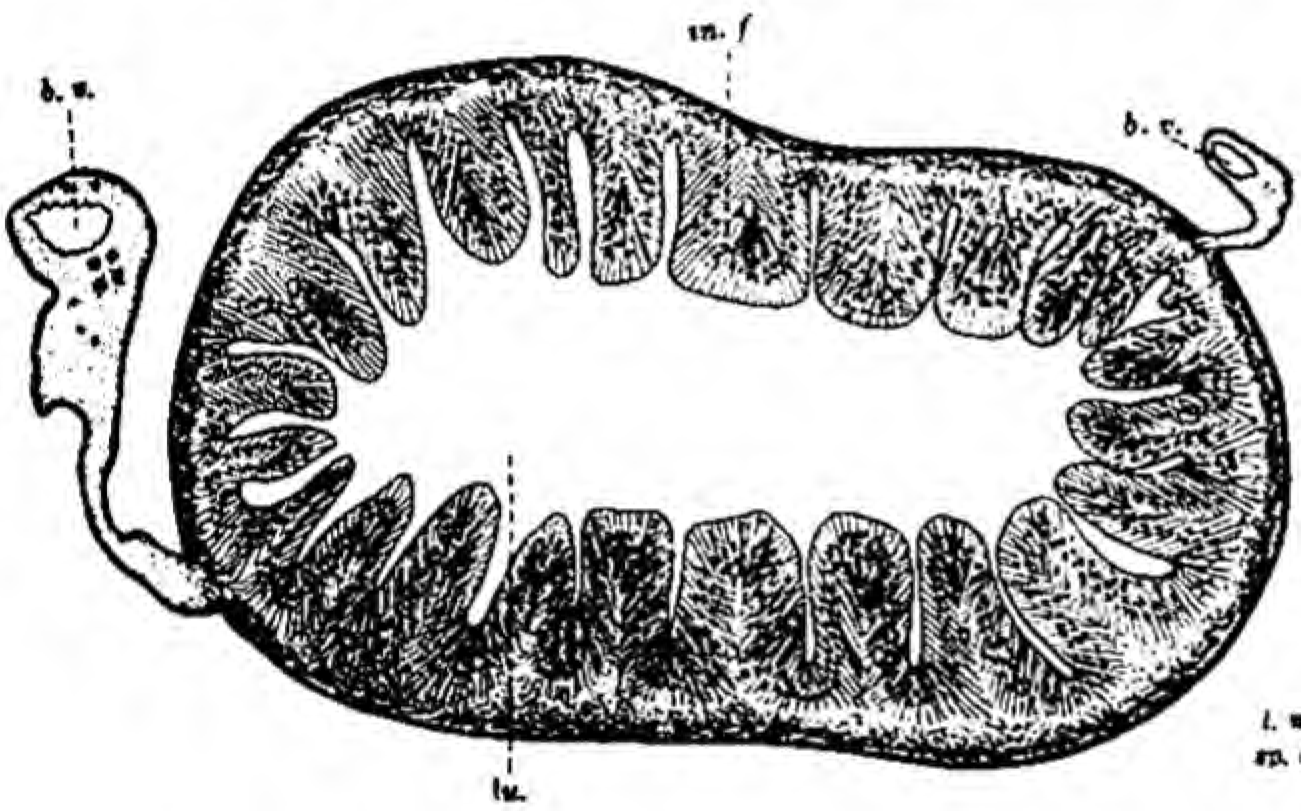


Fig. 22.

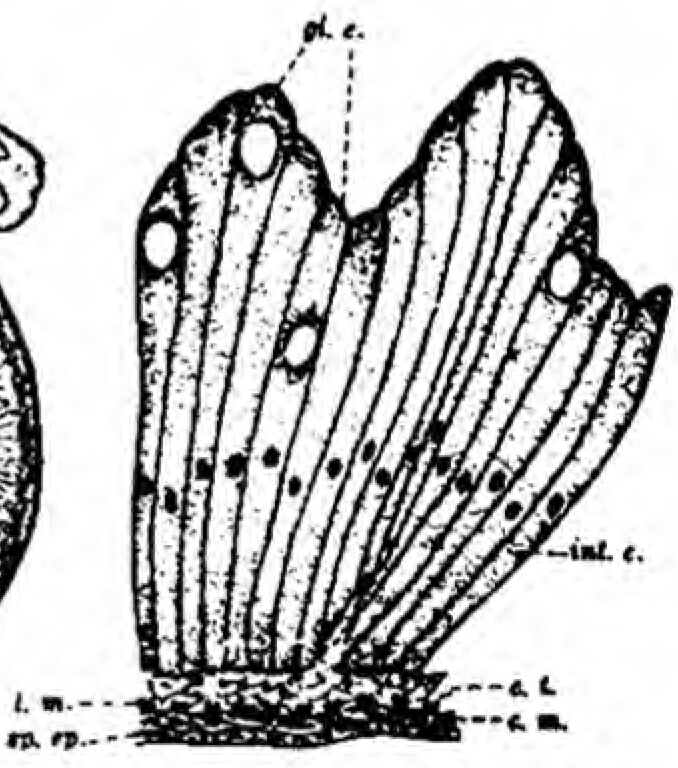


Fig. 23.

Fig. 22—A transverse section of the intestine. *b. v.*, blood-vessel; *in. f.*, intestinal fold; *u.*, lumen of the intestine. (× cir. 38)

Fig. 23—A section of a part of the intestine. *c. m.*, circular muscle layer; *c. t.*, connective tissue layer; *gl. c.*, gland-cells; *int. c.*, ordinary intestinal cell; *l. m.*, longitudinal muscle layer; *sp. ep.*, splanchnic epithelium. (× cir. 130)

canal, but they are much more numerous in the pharynx and the rectum than in the other regions of the alimentary canal.

Physiology of feeding and digestion.

Sea-urchins are omnivorous animals. *Echinus esculentus* feeds on the brown fronds of *Laminaria* and the small worms and molluscs found in abundance thereon, while *Strongylocentrotus* and *Stomopneustes* have been seen to capture the crustacean *Squilla*.

Phagocytic amoebocytes are found within the epithelium of the gut and also wander freely in its lumen; these are possibly the principal agents of absorption and of some intra-cellular digestion.

These amoebocytes are filled with dark granules which tend to disappear in a starved sea-urchin. Extra-cellular digestion is well developed, and all types of enzymes—sucroclastic, proteoclastic and lipoclastic—are present in the stomach of the Echinoidea, which forms the secretory and digestive region of the gut. The sea-urchin would thus seem to digest carbohydrates, proteins and fats with equal ease. Absorption of digested food appears to be confined to the intestinal region of the gut. It is difficult to be certain as to what extent intra-cellular digestion,

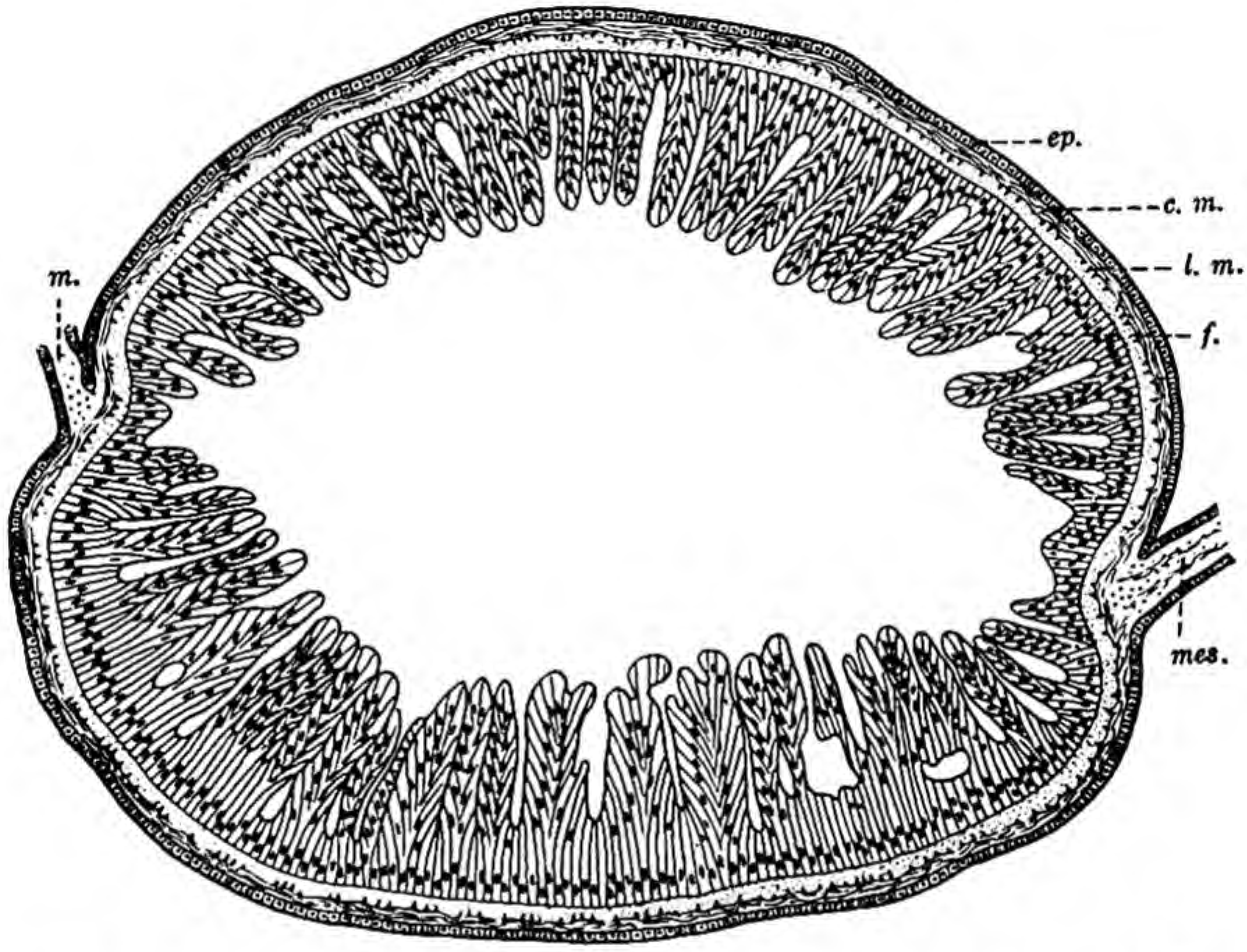


Fig. 24—A transverse section of the rectum. *c. m.*, circular muscle layer: *ep.*, epidermis; *f.*, longitudinal folds in the rectum; *l.m.*, longitudinal muscles layer; *m.*, connecting membrane between the rectum and the stone-canal; *mes.*, mesentery (× cir. 50).

apart from that in phagocytic amoebocytes, occurs in the Echinodermata[1].

1 Yonge, C. M.—"Evolution and adaptation in the digestive system of the Metazoa". Biological Reviews, Vol. 21, No. 1, 1937.

CHAPTER V

THE COELOM AND ITS DERIVATIVES

At a very early stage of development the coelom of the sea-urchin becomes divided into *four* separate compartments which lead to the formation of the various parts of the coelom of the adult. In the adult the coelom consists of: (1) the general body-cavity or perivisceral coelom, (2) the peripharyngeal or lantern-coelom, of which the perihaemal canals are outgrowths, (3) the water-vascular system, (4) the axial coelom, (5) the aboral ring-coelom, and (6) the madreporic vesicle. Besides these parts of the coelom, the gonads (chapter X) are outgrowths of the coelomic wall and so are Lange's nerves in the Asteroidea (chapter VIII).

(1) *The perivisceral coelom.*

The *general body-cavity* is very spacious and occupies the greater part of the animal within the test (fig. 19). It is filled with coelomic fluid which was formerly believed to be mere sea-water but is now known to be a denser fluid with a small amount of albuminous material in solution. The fluid is slightly alkaline in reaction and contains amoeboid corpuscles called *amoebocytes* or *arthrocytes* as well as *pigment-corpuscles.* Microscopic examination of freshly drawn coelomic fluid shows four types of corpuscles as shown in fig. 25. The *first* type are colourless amoeboid bodies with a finely granulated cytoplasm, a rounded nucleus, and very slender anastomosing pseudopodia. Some of these corpuscles may come together and form plasmodia. The *second* type are colourless amoeboid cells with densely packed granules and a rounded nucleus. These are usually provided with a single short blunt pseudopodium. Corpuscles of the *third* variety

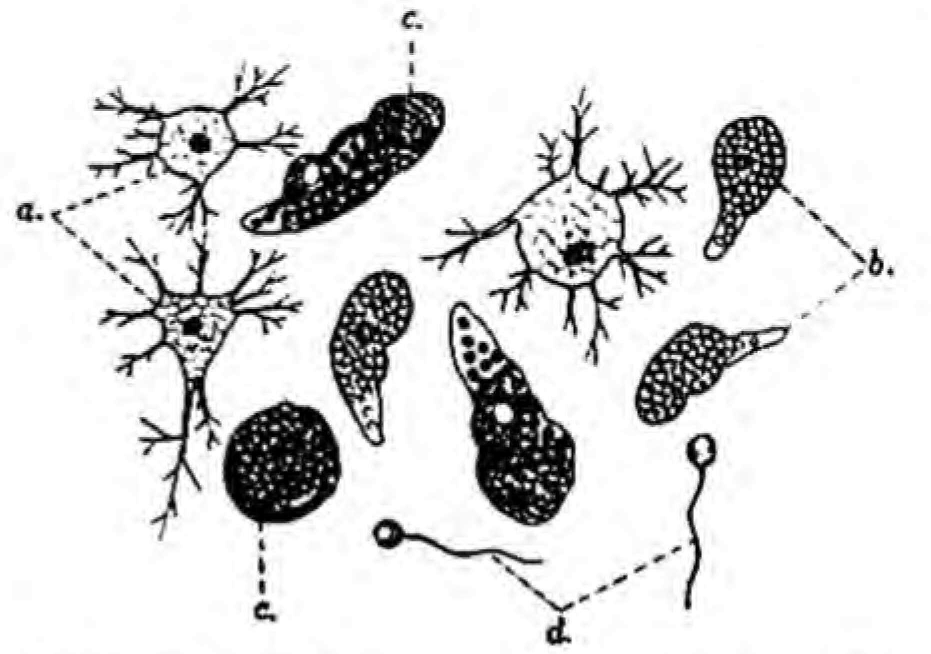


Fig. 25—Different types of corpuscles found in a drop of fresh coelomic fluid. *a.*, amoebocytes; *b.*, granulated corpuscles; *c.*, pigment-corpuscles; *d.*, ciliated cells.

resemble those of the second but are deeply pigmented and possess one or two blunt pseudopodia. The *fourth* kind floating in large numbers in the coelomic fluid cannot be called amoeboid, as they are sperm-like in appearance with a globular nucleated head and a long vibratile tail. The amoebocytes probably collect soluble waste material from the coelomic fluid or from the fluid in the water-vascular system; the waste material is carried by them either in a liquid form in the vacuoles of their cytoplasm or as granules or crystals. The chemical nature of these excretions has not yet been determined. These amoebocytes eventually penetrate the dermis and either degenerate there forming pigment, or escape to the exterior through the walls of the gills. In addition to their excretory function, the amoebocytes are also believed to be phagocytic and to act as store-houses of reserve material.

(2) *The lantern-coelom and the perihaemal canals.*

The *lantern-coelom* surrounds the pharynx and the lantern-apparatus and is cut off from the general perivisceral coelom by a septum outside the lantern. The jaws of the lantern actually lie within the outer wall of the lantern-coelom, and this wall has been appropriately named by Valentine the "lantern membrane". Morphologically the lantern-coelom represents the enlarged outer perihaemal ring of the Asteroids, the inner perihaemal ring of the starfish being absent in the sea-urchin. At an early stage of development, five double perihaemal canals are given off radially from the five corners of the lantern-coelom and run outwards between the radial nerve-cord and the water-vessel of each ambulacrum. But in the adult, unlike the case in starfish, the two perihaemal canals of each radius fuse into one and are completely closed off from the lantern-coelom. Each radial perihaemal canal thus becomes an independent part of the coelom extending the whole length of the radius and giving off, on either side, branches which accompany the nerves to the bases of the tube-feet.

In some of the Echinoidea like Cidaroida and Echinothuridae, the lantern-coelom gives off five small sacs which project upwards into the perivisceral coelom; these sacs were first noticed by Stewart and are therefore known as *Stewart's organs* or *internal gills*. In forms like *Asthenosoma* these internal gills attain a large size, but in *Salmacis* they are absent altogether. In *Salmacis*, however, the lantern-coelom is in communication with the

external gills or *branchiae* (figs. 1, 35 and 36) which lie on the outer surface of the body in the inter-radii just beyond the peristomial region.

The fluid in the perihaemal canals is similar in composition to the coelomic fluid but is said to contain a greater proportion of albumen. In the Echinoidea the perihaemal system is closed and no definite circulation has been observed. We are not certain about the function of this system, but as it runs closely along the nervous system, it is believed that it gives protection and nourishment to the nerve-trunks.

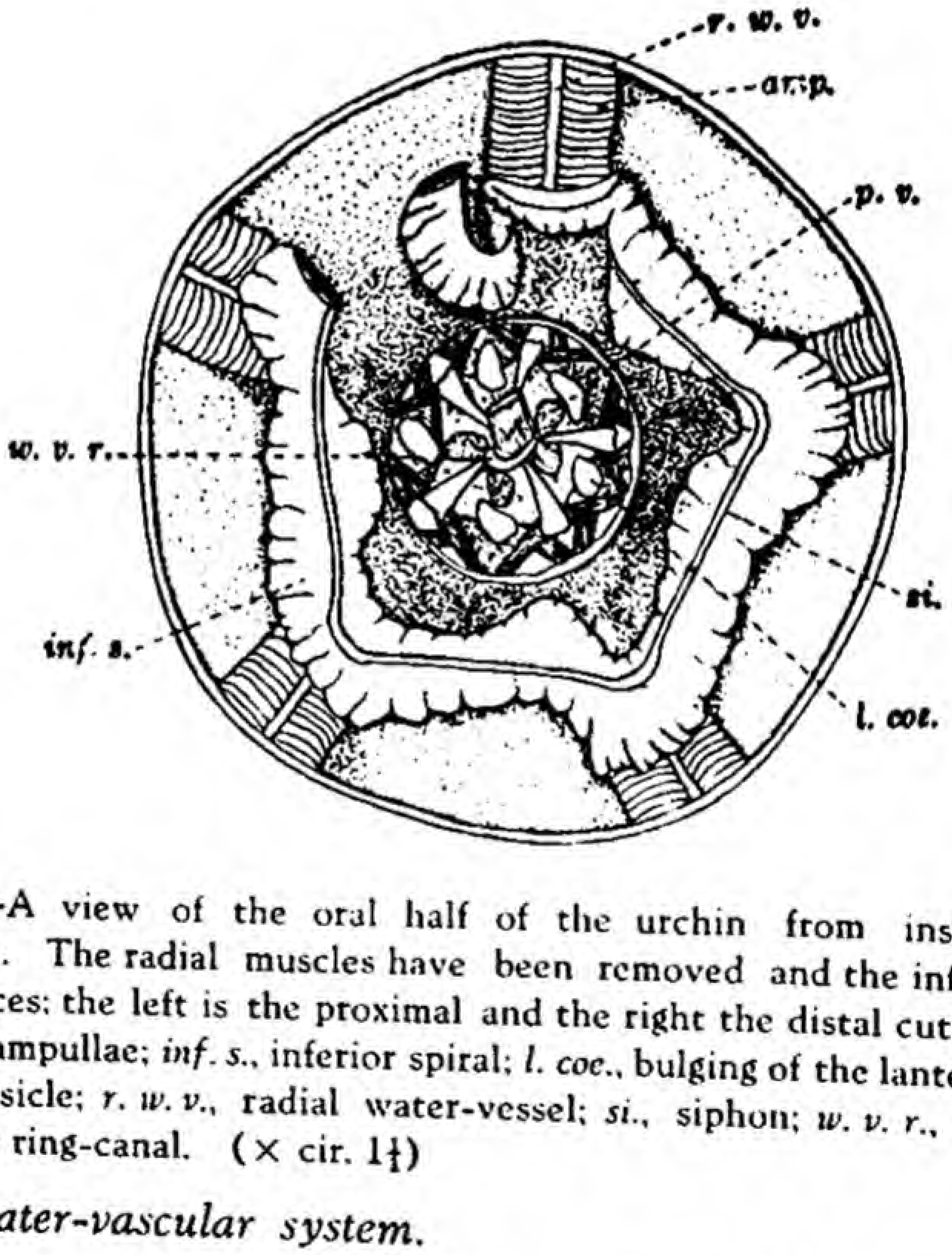


Fig. 26—A view of the oral half of the urchin from inside (semi-diagrammatic). The radial muscles have been removed and the inferior spiral cut at two places: the left is the proximal and the right the distal cut end of the spiral. *amp.*, ampullae; *inf. s.*, inferior spiral; *l. coe.*, bulging of the lantern-coelom; *p.v.*, Polian vesicle; *r. w. v.*, radial water-vessel; *si.*, siphon; *w. v. r.*, pharyngeal water-vascular ring-canal. (× cir. 1¼)

(3) *The water-vascular system.*

The water-vascular system consists of: (1) the pharyngeal ring-canal with its five Polian vesicles, (2) five radial canals with their ampullae and tube-feet, (3) the stone-canal, and (4) the madreporitic plate.

The pentagonal *pharyngeal ring-canal* (figs. 26 and 27) surrounds the pharynx at the upper end of the Aristotle's lantern and lies just beneath the pentagonal muscular ring formed of thin sheets of muscles of the radial pieces (compasses) of the lantern.

The lumen of the ring-canal is lined with a definite layer of ciliated cells. Attached to the ring-canal are five small sac-shaped structures called the *Polian vesicles* (fig. 27), which are inter-radially situated and have a spongy lumen. Externally each vesicle shows a partial division into two and each division is again irregularly sub-divided. C-shaped spicules are very common in the walls of these vesicles. In Echinoids the Polian vesicles are usually five in number but this number may be exceeded as in *Echinodiscus biforis*. They have usually a rich network of vascular tissue which springs from the underlying blood-vascular ring. According to Hamann the function of the Polian vesicles is to produce 'amoebocytes' (wandering cells) which float in the fluid of the water-vascular system. Alternating with the Polian vesicles arise five *radial water-vascular canals* (fig. 27) which at first run downwards for a very short distance closely pressed against the sides of the pharynx, and then turn outwards passing beneath the rotulae and running downwards along the spaces between the two halves of adjoining pairs of alveoli; thence they emerge through the bridges of the auricles and run outwards and upwards along the middle of each ambulacral area on the inner surface of the test; finally they reach the ocular plates, where each canal ends blindly in a small terminal tentacle (fig. 36). Beyond the peristomial region, i. e. outside the perignathic girdle of the auricles, each radial vessel gives off a series of *transverse vessels* alternately on either side (fig. 27); each of these transverse vessels on the two sides ends in a *tube-foot*. A tube-foot consists of a rounded *ampulla* and a long *stalk* which is provided with a terminal *sucker* supported by a calcareous *sucker-plate* (figs. 28 and 29). The ampulla lies within the test while the stalk is situated on the outside, but the two are connected with each other through two very short canals which pierce the ambulacral ossicle through a pair of apertures. Each pair of apertures on the ambulacral ossicle therefore corresponds to a tube-foot, so that there are three transverse vessels and three tube-feet on each ambulacral plate (fig. 9). The wall of a tube-foot consists of an external epithelium, a layer of elastic tissue, a layer of nervous tissue, a layer of muscles, and an internal layer of ciliated epithelium (fig. 30). In a young urchin, each tube-foot perforates the test by a single pore only, but as the animal grows, a small calcareous piece develops at the base of the stalk, which divides the stalk at this place into two rootlets which unite again as they pass into the ampulla within the test (fig. 28).

The ampullae are perfectly transparent in the living condition and can be easily seen when the test is opened and examined from inside (fig. 26). The wall of an ampulla consists of an outer layer of coelomic epithelium, a connective tissue layer, a muscular layer, and an internal layer of ciliated epithelium. A few muscle-fibres run from one side of the wall to the other across the cavity of the

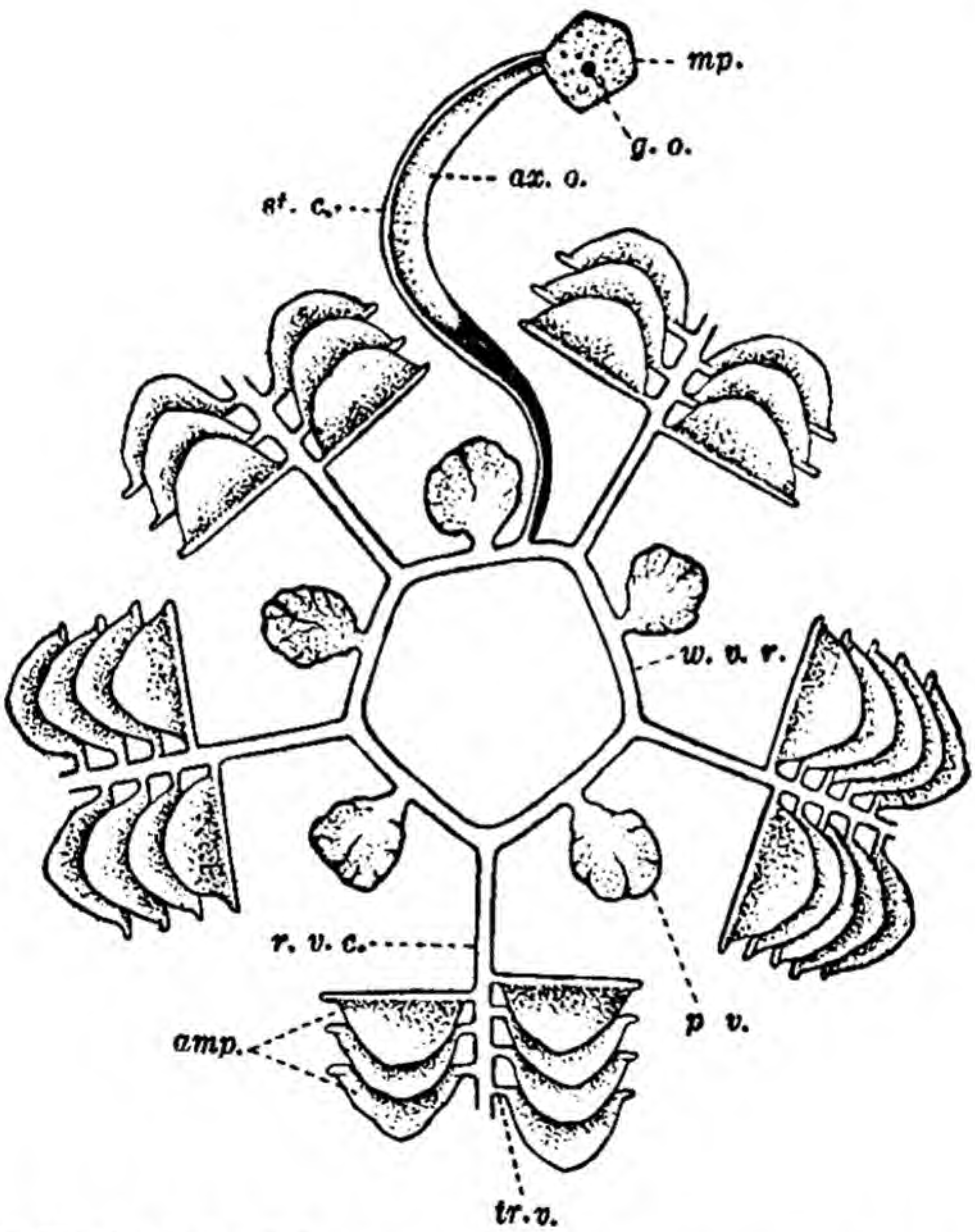


Fig. 27—A diagram of the water-vascular system. *amp.*, ampullae; *ax.o.*, axial organ surrounding the axial coelom; *m. p.*, madreporitic plate; *p. v.*, Polian vesicle; *st. c.*, stone-canal; *tr. v.*, transverse vessel; *w. v. r.*, water-vascular ring-canal.

ampulla. The tube-feet are capable of a great deal of extension and contraction, and when fixed in preserving reagents, their walls become thrown into a large number of folds.

The division of the connecting canal between the ampulla and the stalk of a tube-foot into two canals in the adult is an adaptation to the respiratory function of the tube-feet. The

internal ciliated lining produces a current which proceeds from the stalk to the ampulla by one canal and comes back to the stalk by the other; the water in the tube-foot absorbs oxygen from the seawater and the oxygenated water is conveyed into the ampulla whence the oxygen diffuses into the perivisceral coelom for respiration.

Besides the ordinary ambulatory and respiratory tube-feet there are five pairs of radially placed *buccal tube-feet* (Pages 8 and 9), which are short and are probably used for tasting food. These also take their origin, like the other tube-feet, from the radial vessels. Specially modified respiratory tube-feet, as are found in *Echinocardium*, are absent in *Salmacis*.

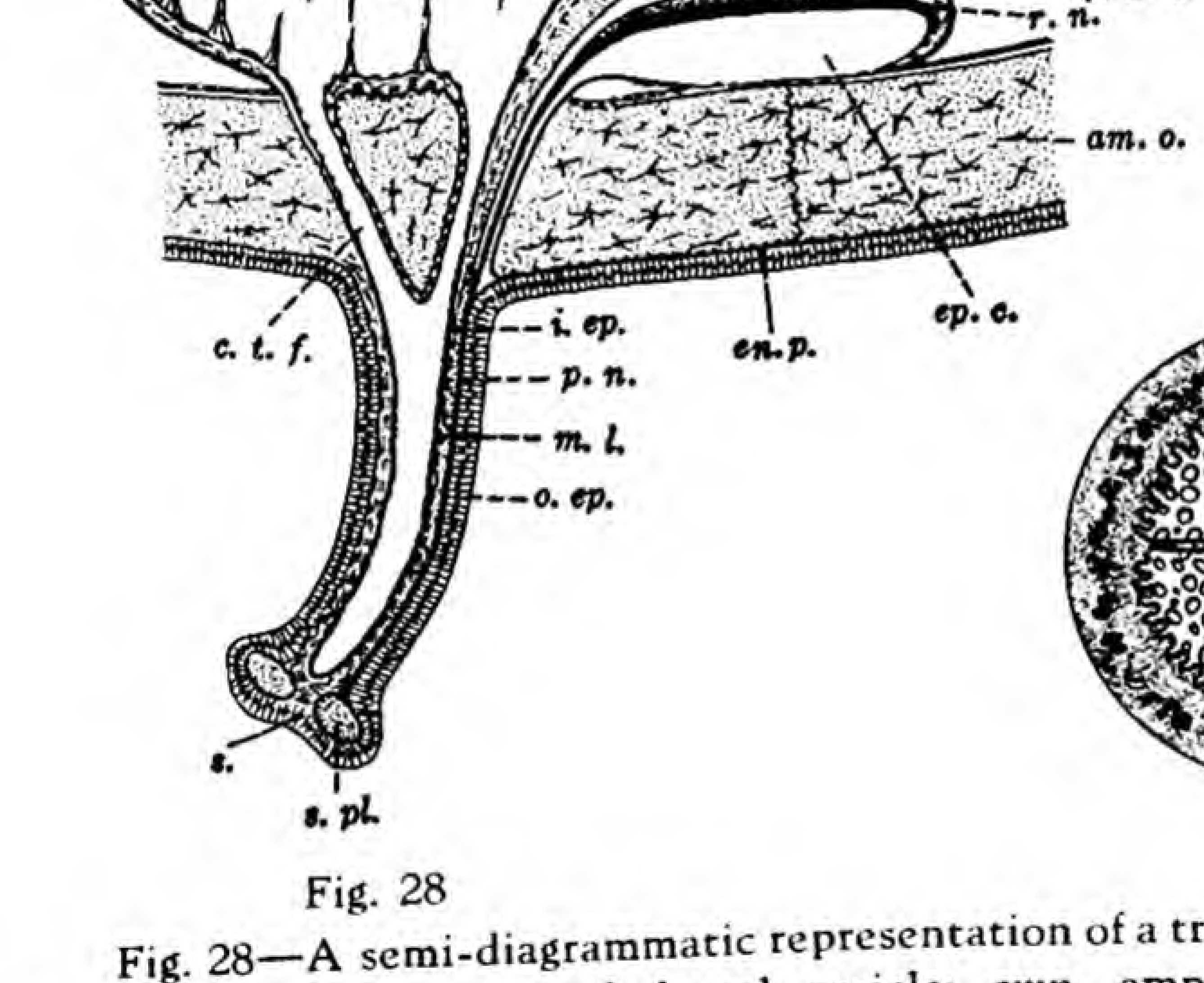


Fig. 28

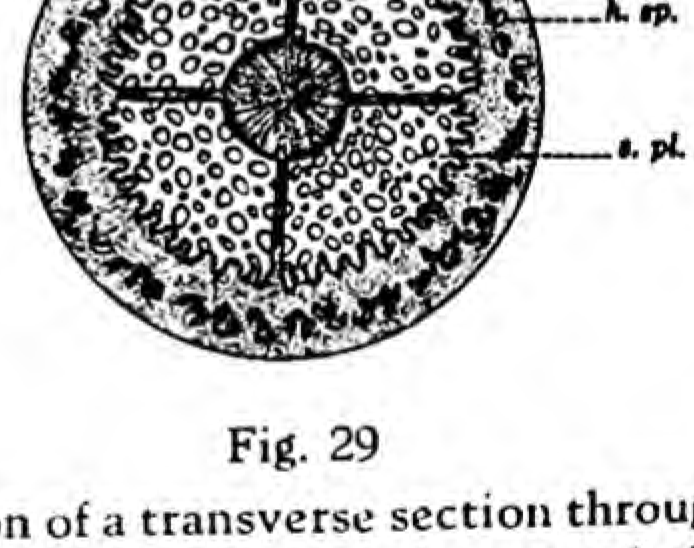


Fig. 29

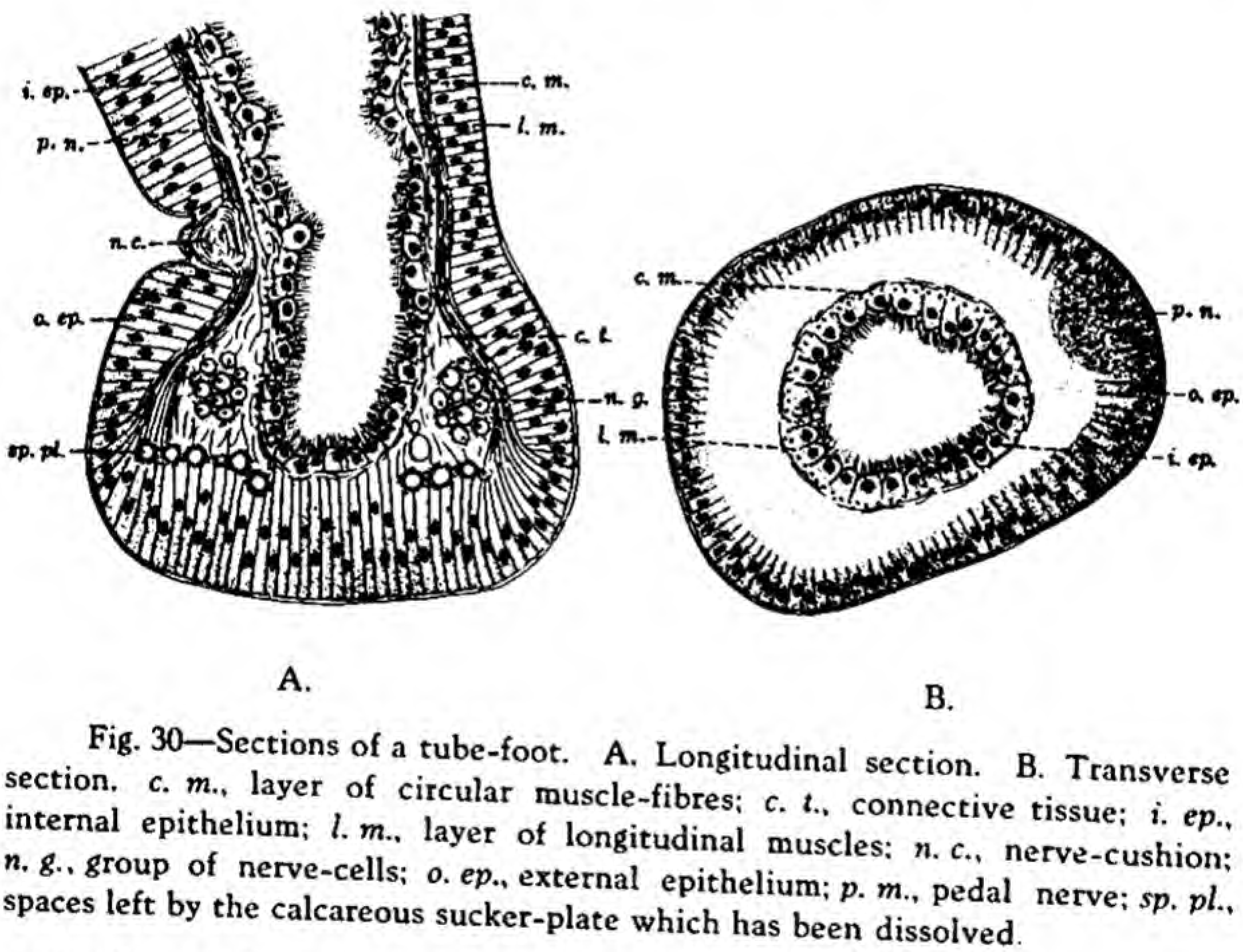
Fig. 28—A semi-diagrammatic representation of a transverse section through an ambulacrum. *am. o.*, ambulacral ossicle; *amp.*, ampulla; *c. t. f.*, one of the two canals for the tube-foot; *en. p.*, ectoneural (sub-epithelial) plexus; *ep. c.*, epineural canal; *i. ep.*, internal epithelium; *m. l.*, muscular layer; *o. ep.*, outer epithelium; *r. b. v.*, radial blood-strand; *r. n.*, radial nerve; *r. p. h. c.*, radial perihaemal canal; *r. w. v.* radial water-vessel; *s.*, sucker; *s. pl.*, sucker-plate; *v.*, valve.

Fig. 29—Sucker of a tube-foot. *h. sp.*, bihamate spicule; *r. s.*, rim of sucker; *s. pl.*, sucker-plate showing a central membranous part and the four pieces composing the skeletal plate.

From one of the five sides of the water-vascular pentagon springs the *stone-canal* (figs. 27 and 36), which is a narrow tube running vertically upwards and closely following the course of the oesophageal region of the alimentary canal. Aborally it opens into a closed coelomic space, the *madreporitic ampulla*, placed

immediately beneath the perforated madreporite (figs. 32 and 36). The stone-canal is well developed and has thick porous walls with a system of circular muscles and a large number of spicules; its inner surface is thrown into folds projecting into the lumen of the canal (fig. 33).

Various views have been held with regard to the working of the water-vascular system, but the most accepted view at present is given here. The entire system is ciliated and a current of water is constantly entering through the madreporitic plate into the madreporitic ampulla, whence it passes through the stone-canal into the pharyngeal ring-canal. From this ring-canal the water is carried to each of the five radial water-vessels, and thence to the



A. B.

Fig. 30—Sections of a tube-foot. A. Longitudinal section. B. Transverse section. *c. m.*, layer of circular muscle-fibres; *c. t.*, connective tissue; *i. ep.*, internal epithelium; *l. m.*, layer of longitudinal muscles; *n. c.*, nerve-cushion; *n. g.*, group of nerve-cells; *o. ep.*, external epithelium; *p. m.*, pedal nerve; *sp. pl.*, spaces left by the calcareous sucker-plate which has been dissolved.

ampullae and the tube-feet. At the entrance into each ampulla, a *valve* (fig. 29), which allows water to pass from the radial water-vessel into the ampulla but not *vice versa*, has been observed to occur in other Echinoids. Such a valve is probably also present in *Salmacis*. The walls of the ampullae and tube-feet have well-developed muscular and elastic fibres; when therefore, the ampullae contract, the contained water is pumped into the tube-feet which consequently become tense and stretch out; as their suckers come into contact with a rocky surface or with the

glass sides of an aquarium, the central plate of each sucker is raised and a vacuum is formed between the sucker and the point of attachment, with the result that the outside water presses on the rim of the sucker and brings about a firm attachment of the sucker to the substratum. When the ampulla relaxes, the water from the tube-foot rushes back into the ampulla, as a result of which the tube-foot becomes shorter, and so pulls the animal towards the place of attachment of the sucker. This process of contraction and relaxation of ampullae and the consequent extension and shortening of the stalks of the tube-feet is repeated in the successive tube-feet of the ambulacra. In this way, by the concerted and repeated action of the ampullae, tube-feet and their suckers, movement is brought about in any desired direction. Locomotion is very slow and is effected by a series

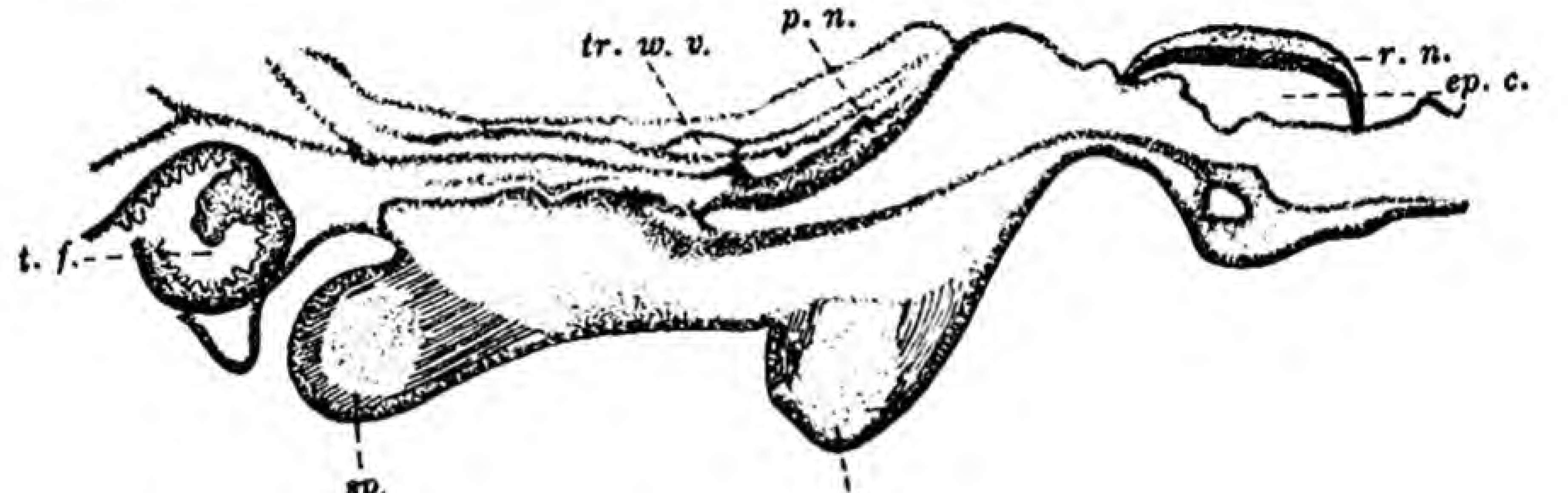


Fig. 31—A section through an ambulacrum. *ep. c.*, epineural canal; *p. n.*, pedal nerve; *r. n.*, radial nerve; *sp.*, spine; *t. f.*, tube-foot; *tr. w. v.*, transverse water-vessel. (× cir. 26).

of jerks as can be seen by watching the movements of a living sea-urchin. The tenacity of attachment of the suckers is so great as to make it possible to lift a medium-sized glass-vessel containing a sea-urchin by lifting the urchin alone.

Dr. Pantin[1] has proved that the function of the stone-canal is to keep up the hydrostatic pressure of the water-vascular system. When a tube-foot is exserted and is distended with fluid, a certain amount of fluid diffuses into the sea; this loss is made good by an inflow from the ampulla; the loss in the ampulla is restored by an inflow from the radial water-vascular canal, which in turn receives its supply from the ring-canal, and ultimately from the stone-canal. The stone-canal is constantly being supplied with fresh seawater through the pores of the madreporite. By placing large starfishes in shallow dishes with clean seawater, so that

1 Kindly brought to my notice by Prof. E. W. MacBride.

although their under sides were bathed with seawater the madreporites were uncovered, Pantin showed that in two or three days the tube-feet lost all their rigidity.

The Polian vesicles in certain Asteroidea, Ophiuroidea and Holothuroidea are large reservoirs of fluid; they are in fact reserves to keep up the tension of the water-vascular system. In the Echinoidea, however, they are small and thick-walled and seem to have the production of amoebocytes as their function (Pages 34, 43 and 44).

(4) *The axial coelom and the axial organ.*

The *axial coelom*[1] is a narrow elongated canal which accompanies the stone-canal and opens aborally into an enlarged cœlomic chamber called the *madreporitic ampulla* (figs. 32 and 36). On the

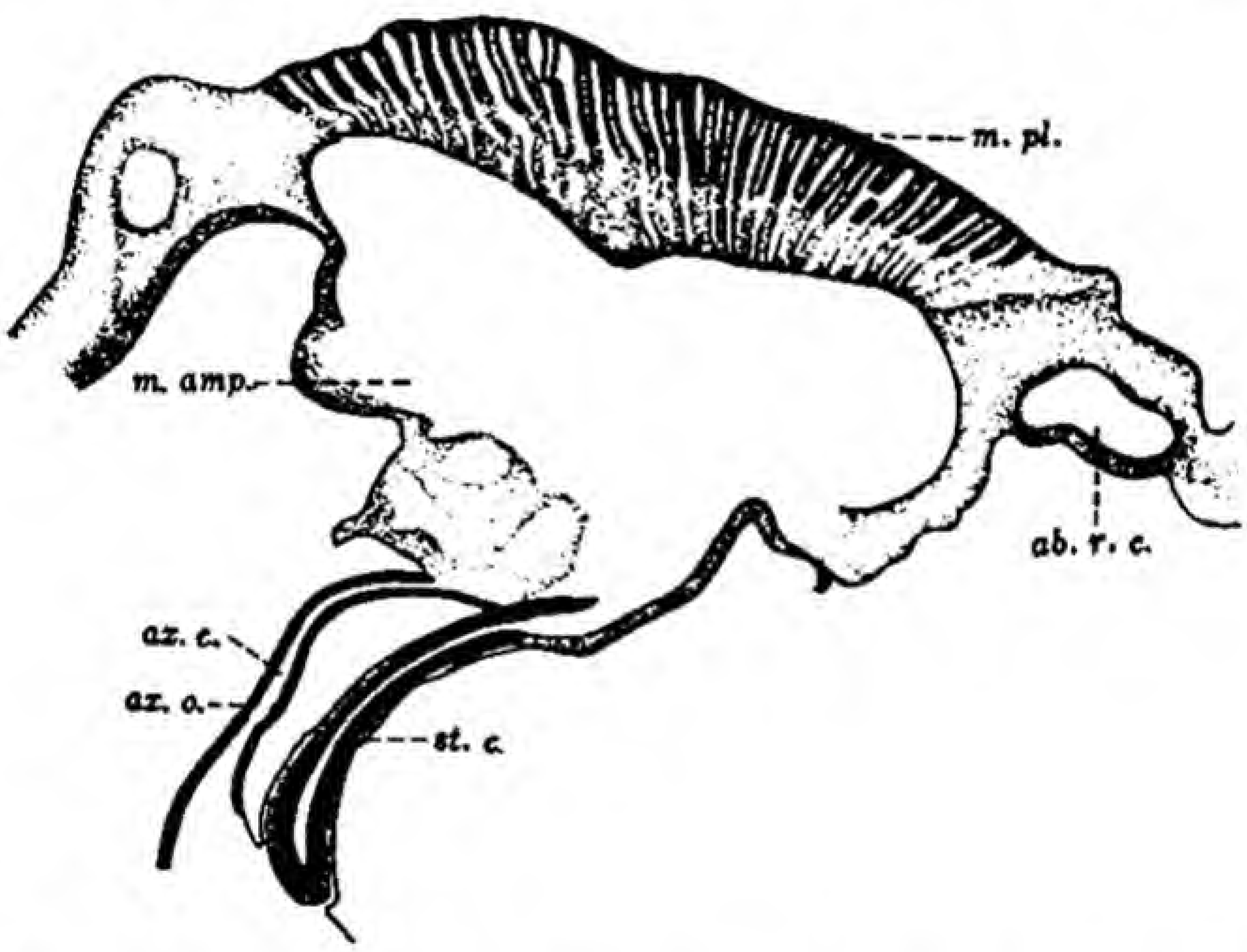


Fig. 32—A section of the madreporitic plate and connected structures. *ab. r.c.*, aboral ring-coelom; *ax. c.*, axial coelom; *ax. o.*, axial organ; *m. amp.*, madreporitic ampulla; *m. p.*, madreporitic plate; *st. c.*, stone-canal. (× cir. 40)

oral side the axial coelom ends blindly at some distance from the water-vascular pharyngeal ring[2]. The wall of the axial coelom is formed of coelomic epithelium and a thick pigmented tissue with

1 The terms "axial coelom" and "aboral ring-coelom" have been used here in preference to the commonly used terms "axial sinus" and "aboral ring-sinus", as the beginner is liable to misunderstand the latter terms and think that they refer to parts of the blood-vascular system. The terms adopted here emphasise the true nature of these structures and are not liable to be misunderstood.

2 Some workers have stated that the lower end of the axial coelom opens into the water-vascular ring-canal but this view is not generally accepted.

cells and fibres; this specialised wall is called the *axial organ*, *dorsal organ* or *genital stolon*. The axial organ (fig. 33), therefore, is really the surrounding thickened and pigmented wall of the axial coelom produced into an *internal ridge* which runs all along its length and projects into the lumen of the axial coelom. The axial organ consists chiefly of connective tissue packed with cells containing rounded nuclei and radiating processes which join to form a regular meshwork. The outer part of the axial organ, often designated as the *cortex*, is formed

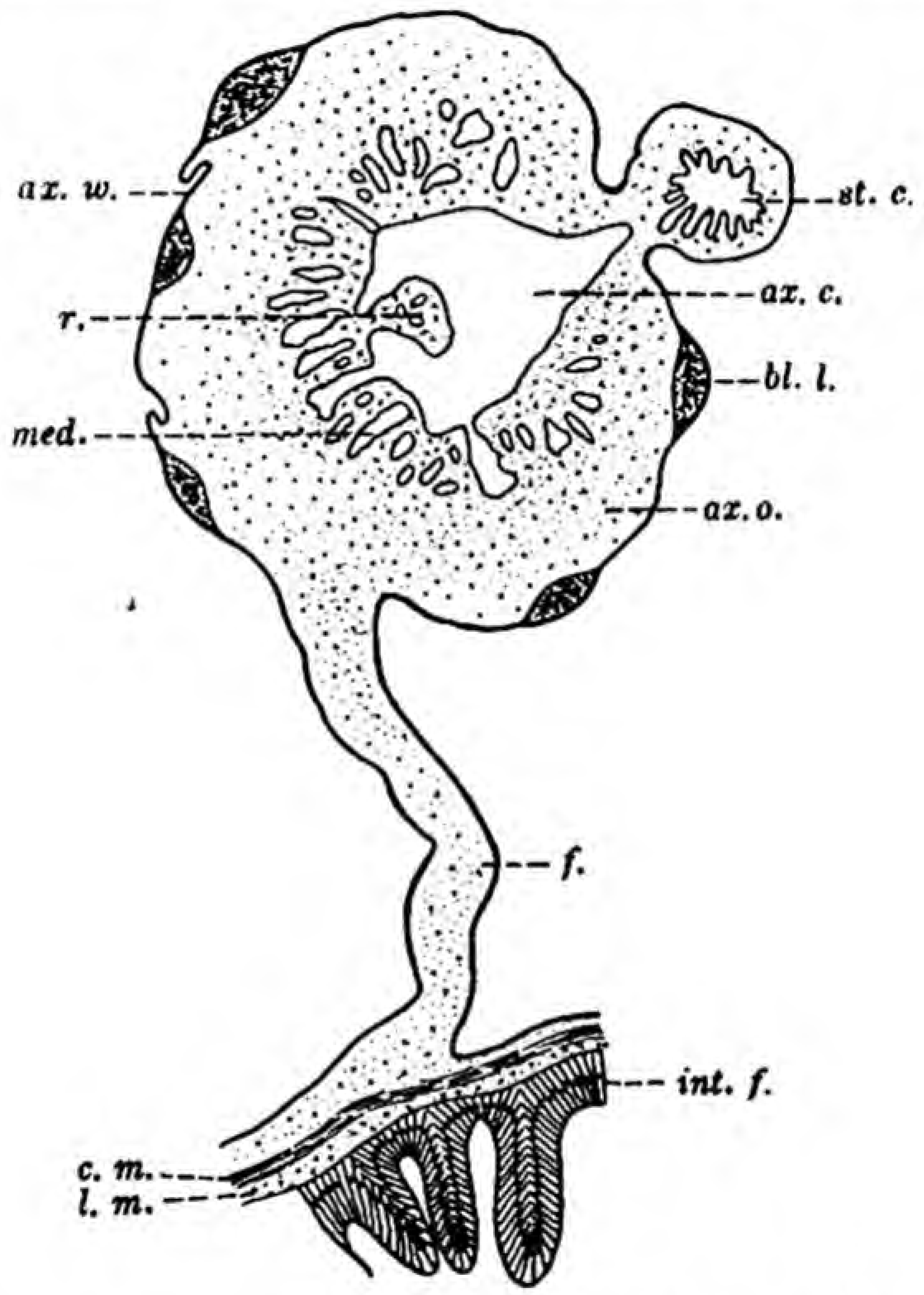


Fig. 33—A section passing through the axial coelom, axial organ and a part of the intestine. *ax. c.*, axial coelom; *ax. o.*, axial organ; *ax. w.*, outer wall of the axial coelom and organ; *bl. l.*, blood-lacuna; *c. m.*, circular muscle layer; *f.*, mesenterial fold between the intestine and the axial coelom and stone-canal; *int. f.*, intestinal epithelium produced into folds; *l. m.*, longitudinal muscle layer; *med.*, medulla of the axial organ; *r.*, internal ridge of the axial organ; *st. c.*, stone-canal. (× cir. 50).

of denser material than the inner, which is called the *medulla* and contains numerous inter-communicating spaces (fig. 33). Peripherally just beneath the enveloping membrane of the axial coelom several blood-lacunae can be seen. MacBride has shown by a study of its development that the axial organ represents the

genital stolon connected at its aboral end with the *circular genital rachis* which lies within the aboral ring-coelom and from which the genital organs are developed (fig. 34). Naturally, as the swelling of the genital organs is periodic, in slack times some of the cells of the stolon degenerate and form the pigmented tissue of the axial organ[1].

The relationship between the madreporitic plate, the stone-canal, and the axial coelom and organ is instructive. The porous madreporite opens into the madreporitic ampulla (fig. 32) lying immediately beneath it. The ampulla leads below into the axial

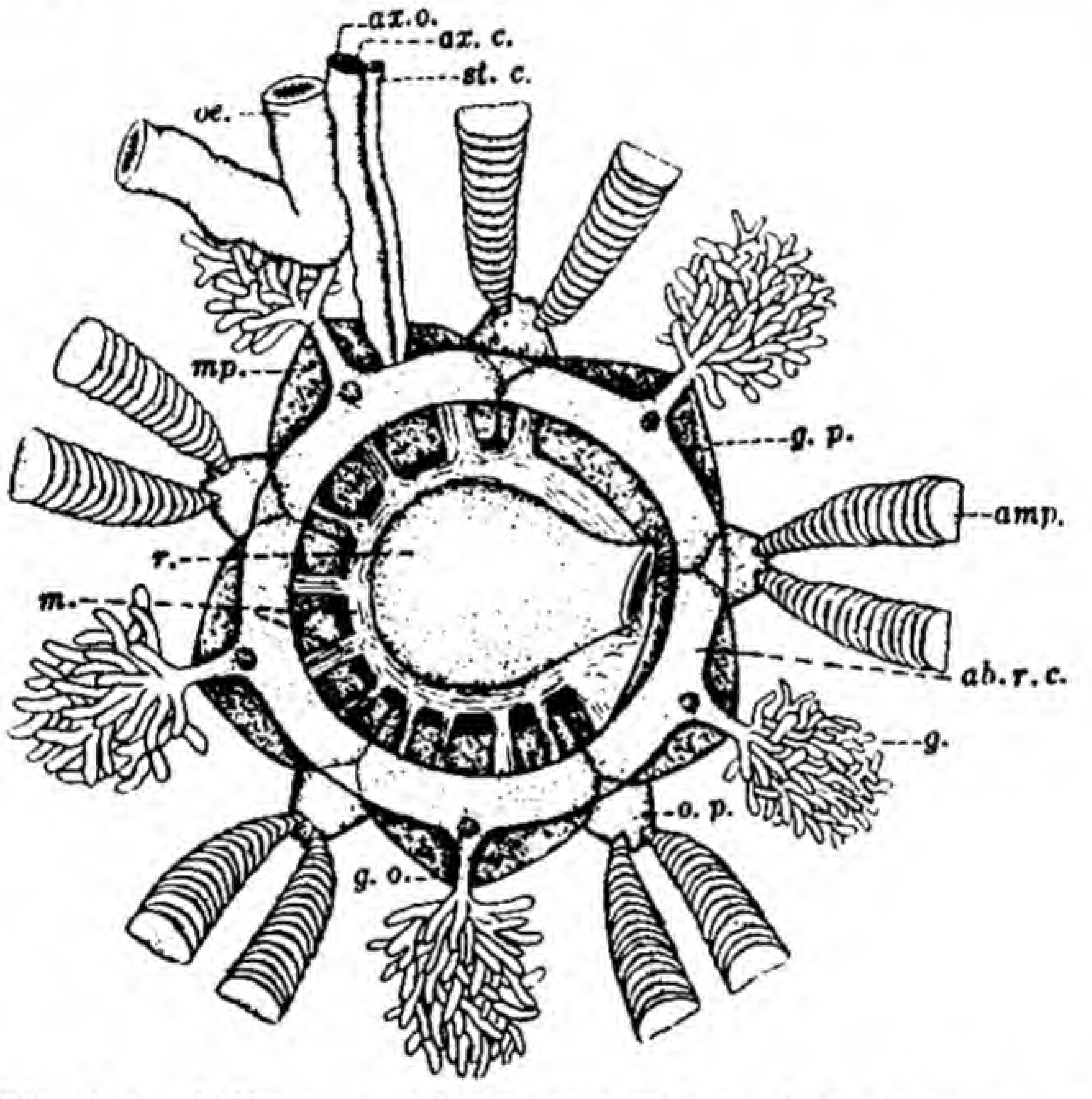


Fig. 34—A semi-diagrammatic representation of the disposition of the aboral ring-coelom, rectum, and the associated structures at the aboral pole. *ab. r. c.*, aboral ring-coelom; *amp.*, ampulla; *ax. o.*, axial organ; *ax. c.*, axial coelom; *g.*, gonad; *g. a.*, genital aperture; *g. p.*, genital plate; *m.*, muscles; *m. p.*, madreporitic plate; *oe.*, oesophagus; *o. p.*, ocular plate; *r.*, rectum; *st. c.*, stone-canal.

coelom (the canal "aquifere annexe" of Prouho) on the one hand, and into the stone-canal on the other.

(5) *The aboral circular coelom.*

The *aboral circular (ring-) coelom*[2] forms a distinct hollow ring surrounding the rectum (fig. 34). Along its inner walls lie

1 For a full history of the different views that have been held about the *axial organ*, cf. "Echinodermata" in Bronn's Thier-Reich, Bd. 11,1892.

2 The term *aboral circular coelom* is used here in preference to the term *aboral circular sinus* (cf. foot-note 1 on Page 39).

strands of generative cells known as the *genital rachides*. The ring-coelom sends five inter-radial prolongations which terminate in the gonads (fig. 34).

(6) *The madreporic vesicle.*

Close to the madreporitic ampulla is a smaller cavity, the *madreporic vesicle* (Prouho's "espace sous-madreporique"), into which projects the "processus glandularis" or the internal ridge of the axial organ. In *Salmacis* this ridge is best developed in the middle portion of the axial organ but becomes inconspicuous at the two ends.

CHAPTER VI

THE CONNECTIVE TISSUE SYSTEM AND ITS DERIVATIVES

The connective tissue of the Echinodermata is very fluid in character, consisting of a few loose fibres and large inter-cellular spaces. The cells composing this tissue are massed together at several places and in these regions they secrete calcium carbonate material which forms the basis of the calcareous ossicles. In the inter-cellular gaps the *amoebocytes* (*arthrocytes*) wander freely and pass to the outside through the walls of the gills and other soft parts, thus subserving the function of excretion. The blood-vascular system of the Echinoids is closely associated with this connective-tissue, and the blood-vessels are simply portions of the inter-cellular spaces which have no epithelioid lining and have run together.

There is a *blood-vascular ring* surrounding the pharynx and lying immediately beneath the water-vascular ring. This ring-vessel gives off five radial blood-strands which first run vertically downwards on the outer surface of the pharyngeal cushions, and then run outward and upward along the ambulacra, between the water-vessels and the radial perihaemal spaces (fig. 28), and finally terminate at the aboral ends of the ambulacral zones (fig. 36). It should be noted that both the circum-pharyngeal ring and the radial strands are strands of lacunar tissue and should not be regarded as true blood-vessels. The most important blood-strands given off from the ring-vessel are the two blood-vessels, one dorsal and the other ventral, which accompany the oesophagus and the stomach (figs. 19 and 36). The blood-spaces constituting them receive, by exudation from the alimentary canal, a rich supply of coagulable fluid having a rich affinity for stains. This stainable material is pumped by the madreporic vesicle along a fold connecting the stomach and the axial organ (fig. 33). According to MacBride the blood-system of the adult urchin is to be compared to the lymph-vessels ensheathing the human intestine, but instead of forming a network, they become concentrated along two definite lines as dorsal and ventral blood-vessels with a lumen. Connecting these two blood-vessels there are smaller vessels which form plexuses in the digestive tract.

The *amoebocytes* or *wandering cells* have a very general distribution in the body of an Echinoid. In the absence of a definite circulatory system, they play the significant rôle of keeping the different regions in communication with each other. Thus they have the power of taking up and distributing food-material, chiefly of an albuminous nature. The excretory function of the amoebocytes is described on Page 47.

CHAPTER VII

THE RESPIRATORY AND EXCRETORY ORGANS

Respiration in the sea-urchin is effected by the tube-feet, the branchiae, the lantern-coelom, the siphon and to some extent by the alimentary canal. It is probable that the body-surface, wherever it is thin, also aids in respiration.

We have already seen that a current of water is constantly flowing into the ciliated water-vascular system through the perforated madreporite and the stone-canal and that this water continually enters the tube-feet. The *tube-feet* are constantly expanding and contracting and are always bathed in seawater. When the tube-feet are distended, their walls become thin and the water in the stalks absorbs oxygen from seawater and this oxygenated water is conveyed into the ampullae, whence oxygen diffuses into the perivisceral coelom and is carried by the coelomic fluid for respiration to all parts of the body (Pages 35-36). Special respiratory tube-feet as are present on the petaloid ambulacra of the cake- and heart-urchins are entirely absent in *Salmacis*.

The *branchiae* are ten highly branched, thin-walled, hollow structures placed inter-radially around the peristome (figs. 1, 35, and 36) and are always immersed in seawater. The walls of the gills have a structure very similar to those of the tube-feet, with the difference that the muscular layers in the gills are poorly developed. In a living animal the gills can be seen in an expanded condition, and when touched shrink very slowly to a small size. When a piece of fresh gill is removed and examined, the outer surface is seen to be clothed with short but closely set cilia. Sections show that there are external and internal epithelial layers with a layer of connective tissue in between. Scattered in the middle layer and supporting the walls of the gills are numerous C-shaped spicules and reticulate calcareous plates (fig. 35), the former being crowded towards the tips of the gills and the latter towards their bases. The lumina of the gills communicate with lantern-cœlom by means of openings at the bases of the gills (fig. 36), and it has been asserted that these openings can be widened or narrowed in

order to regulate the passage of the fluid from the lantern-cœlom into the gills. By the contraction and relaxation of the *depressor muscles* of the lantern of Aristotle, the coelomic fluid in the lantern-coelom is forced into the branchiae where it absorbs oxygen from the seawater. When, on the contraction of the *radial muscles*, the oxygenated fluid in the gills goes back into the lantern-coelom, oxygen diffuses into the surrounding tissues and into the general coelom (Page 25).

The branchiæ are absent in Cidaridæ and Clypeastroidea. Internal gills or Stewart's organs which are merely radial prolongations of the lantern-cœlom are absent in *Salmacis* but are well developed in such forms as *Cidaris* and *Asthenosoma*, being relatively very large in the last genus.

The *accessory intestine* or *siphon* (page 27) branches off from the oesophagus and after running for a short distance alongside

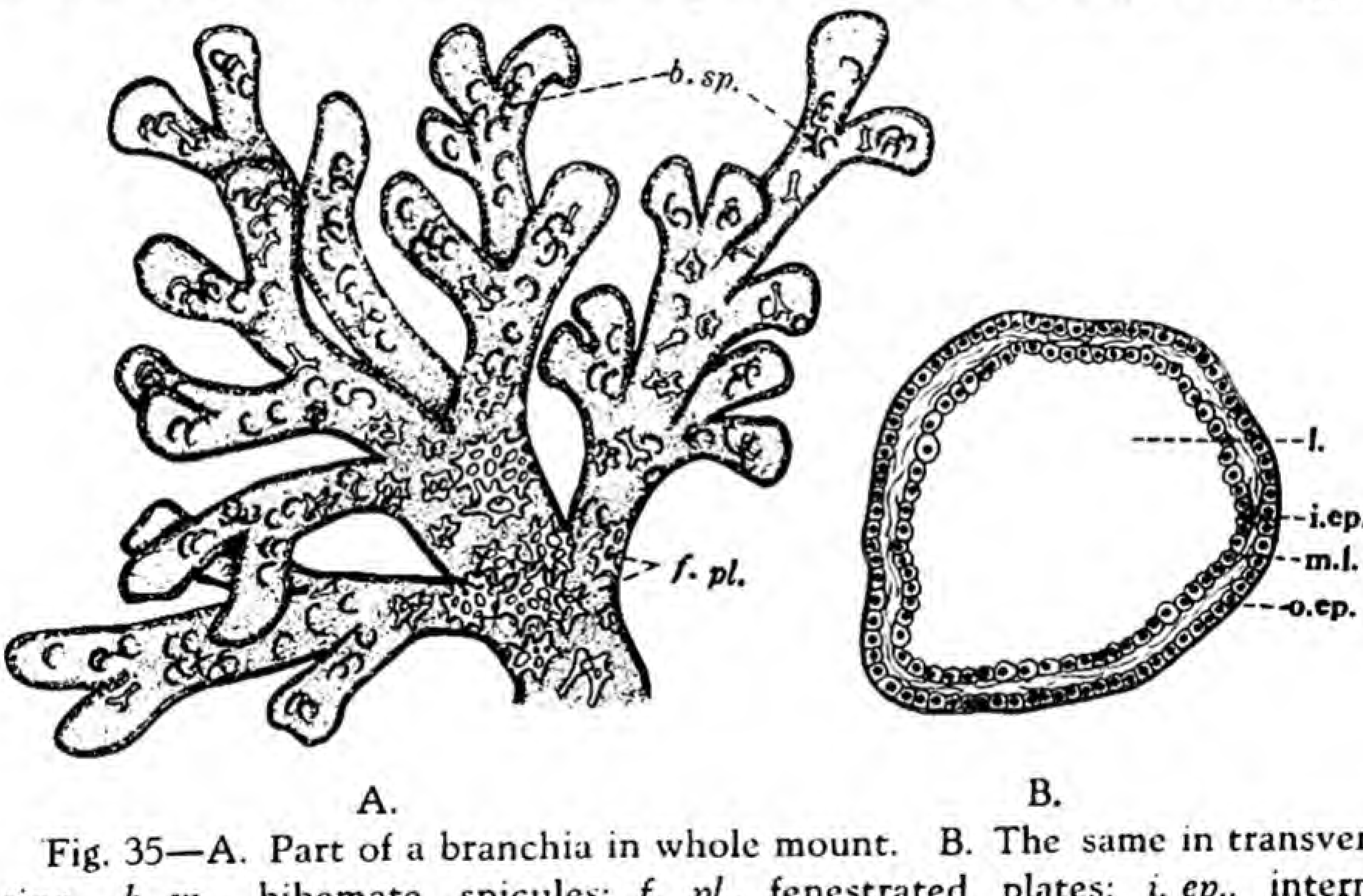


Fig. 35—A. Part of a branchia in whole mount. B. The same in transverse section. *b. sp.*, bihamate spicules; *f. pl.*, fenestrated plates; *i. ep.*, internal epithelium; *l.*, lumen of the branchia; *m. l.*, muscular layer; *o. ep.*, outer epithelium.

the inferior spiral joins it at its other end. The structure of the siphon (fig. 21) is similar to that of the alimentary canal. It has been shown by Perrier that a continuous stream of water from the œsophagus passes through the siphon and comes out into the lumen of the gut at the commencement of the second coil of the alimentary canal. This water is free from food-material which passes direct into the inferior spiral. The walls of the siphon being comparatively thin, exchange of gases between the fluid in the siphon and the slowly moving perivisceral fluid can take place easily. Besides the cilia of the siphon, peristaltic

contractions of the alimentary canal also play an important part in keeping the internal fluids in motion.

Perrier attributes a respiratory function to the alimentary canal as well. When an animal is opened, the alimentary canal is often found filled with seawater. The walls thus become highly stretched and thin with the result that gaseous exchange between the water in the alimentary canal and the cœlomic fluid is facilitated.

MacMunn has described a respiratory pigment in the cells floating in the coelomic cavity of *Echinus esculentus*, *Strongylocentrotus lividus*, etc. The pigment can be extracted by means of alcohol, ether, and chloroform. He has named this pigment *echinochrome*, and distinguishes two forms of the pigment, namely, the *oxyechinochrome* and the *echinochrome* which, according to him, correspond to oxyhæmoglobin and hæmoglobin. He attributes a respiratory function to these pigments, but this view of his has not received general acceptance.

Very little is known about excretion in the Echinoderms, there being no excretory structures of the nature of nephridia in this group. The amoebocytes (Pages 43 and 44) which are generally distributed throughout the body of the sea-urchin are believed to have an excretory function as well. They are phagocytic and ingest bacteria and other foreign bodies and also take up liquid waste-substances. Brownish concretions and crystals and vacuoles containing liquid excretory matter have been seen in these amoebocytes. It is believed that the amoebocytes laden with excretory material either pass out to the exterior through the walls of the branchiae or degenerate within the dermis and form pigment.

CHAPTER VIII

THE NERVOUS SYSTEM

In the Echinodermata the nervous system consists of three divisions: (1) the ventral or *ectoneural*, (2) the deep oral or *hyponeural*, and (3) the *apical* systems. The first is sensory in function, while the other two are motor. Though these three divisions are described separately, it must not be imagined that they are entirely unconnected. It is being recognised more and more that the sensory ectoneural system must be connected with the motor hyponeural and apical systems. All these three divisions, however, are not equally well developed in the different classes of the phylum.

The *ventral nervous system* in *Salmacis* is well-developed and consists of: (1) a circum-oral nerve-ring, (2) five radial nerve-strands and (3) a sub-epithelial nerve-plexus (figs. 28 and 36). The *circum-oral nerve-ring* surrounds the mouth and lies between the peristomial membrane and the Aristotle's lantern. It gives off five *radial nerve-strands*, each of which runs along the inner surface of an ambulacrum. Each radial nerve-strand is formed as a thickening of the roof of the *epineural canal*[1] (fig. 28), which is a closed canal and corresponds to the ambulacral groove of the starfish or the crinoid. The position of the radial nerve in relation to the water-vascular system and the perihaemal canal is shown in figs. 28 and 36. *Transverse nerve-strands* are given off from each radial nerve; some of these, the *pedal nerves* (figs. 28 and 30), accompany the tube-feet to the outside, while others become merged into the *sub-epithelial* (*ectoneural*) *nerve-plexus* (fig. 28) beneath the skin which innervates the spines, pedicellariae, etc. Each radial nerve ends into the tentacle-like termination of the radial water-vascular canal on an ocular plate of the periproct (fig. 36).

The *deep oral* (*hyponeural*) *system* is very poorly developed in the Echinoidea. It takes the form of five nerve-patches which are radial in position and lie partly on the circum-oral nerve-ring and partly at the places of origin of the five radial nerves. There are no radial extensions of these nerve-patches

1 The epineural canal is developed in the larva by the closure of an ectodermal groove along the centre of each radius (MacBride).

along the ambulacra. The nerve-patches consist of nerve-cells and fibres and are separated from the ectoneural nerve-ring by a thin layer of connective tissue. The hyponeural system innervates the muscles that work the lantern-apparatus. In heart-urchins, in which the lantern-apparatus is absent, these nerve-patches also do not exist.

In the Asteroidea the hyponeural system takes the form of double cords running in each of the arms, one on either side of the perihaemal spaces; these

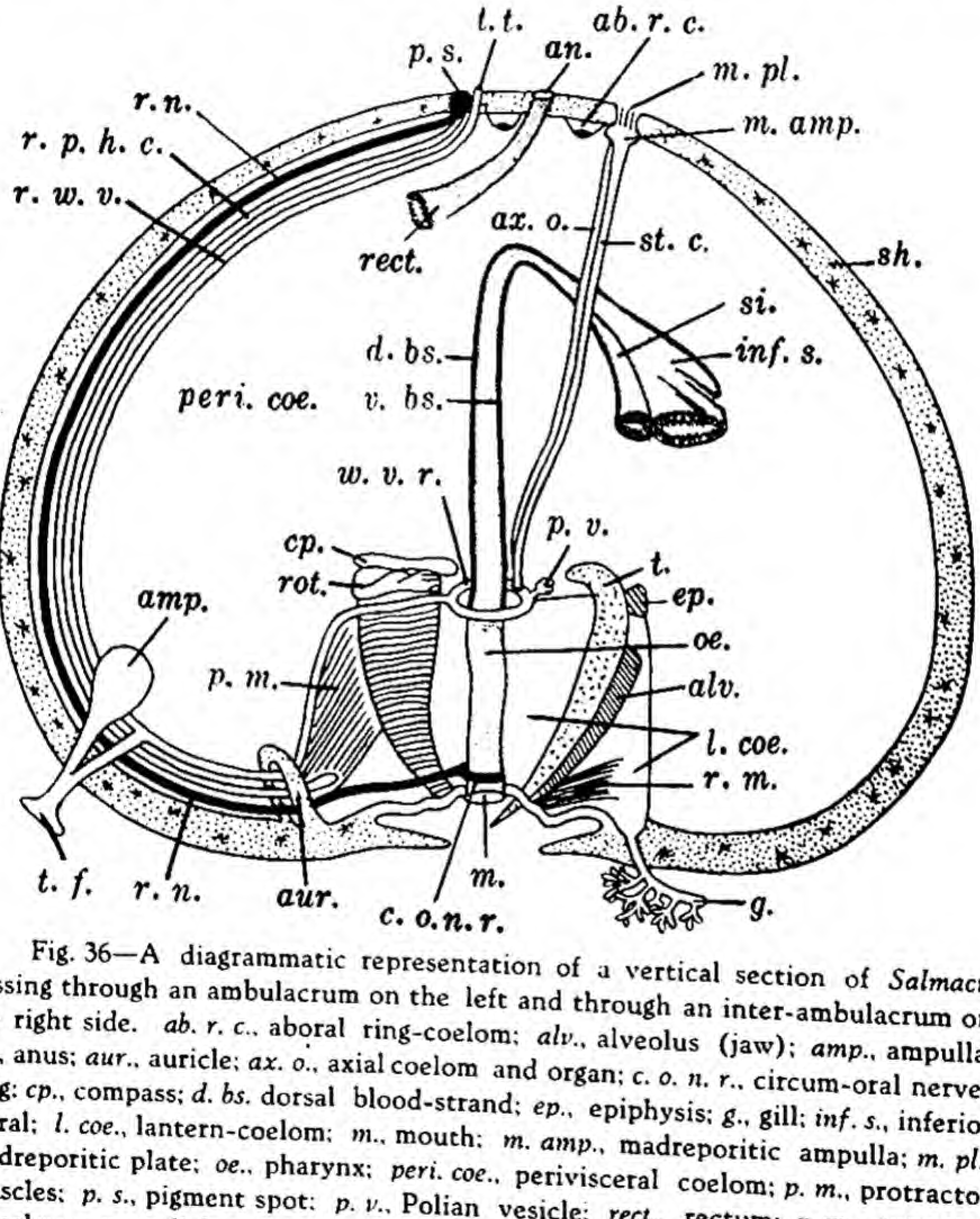


Fig. 36—A diagrammatic representation of a vertical section of *Salmacis* passing through an ambulacrum on the left and through an inter-ambulacrum on the right side. *ab. r. c.*, aboral ring-coelom; *alv.*, alveolus (jaw); *amp.*, ampulla; *an.*, anus; *aur.*, auricle; *ax. o.*, axial coelom and organ; *c. o. n. r.*, circum-oral nerve-ring: *cp.*, compass; *d. bs.* dorsal blood-strand; *ep.*, epiphysis; *g.*, gill; *inf. s.*, inferior spiral; *l. coe.*, lantern-coelom; *m.*, mouth; *m. amp.*, madreporitic ampulla; *m. pl.*, madreporitic plate; *oe.*, pharynx; *peri. coe.*, perivisceral coelom; *p. m.*, protractor muscles; *p. s.*, pigment spot; *p. v.*, Polian vesicle; *rect.*, rectum; *r. m.*, retractor muscles; *r. n.*, radial nerve; *r. p. h. c.*, radial perihaemal canal; *rot.*, rotula; *r. w. v.*, radial water-vascular canal; *sh.*, test; *si.*, siphon; *st. c.*, stone-canal; *t.*, tooth; *t. f.*, tube-foot; *t. t.*, terminal tentacle; *v. bs.*, ventral blood-strand; *w. v. r.*, water-vascular ring. (Adapted from Borradaile, Eastham, Potts and Saunders's "The invertebrata".)

cords are called *Lange's nerves*, and all ten of them appear to be connected with an incomplete nerve-ring round the mouth. The cells forming the hyponeural system are derived from the walls of the perihaemal canals and are therefore coelomic in origin.

The *apical nervous system* is also coelomic in origin and motor in function but is unrepresented in the Echinoids. It is best developed in the Crinoids and less so in the Asteroids, while it appears to be absent in the Ophiuroids, Holothuroids and Echinoids.

A comparison has been instituted by Smith[1] between the corresponding components of the nervous system in the different classes of the Echinodermata. He states that in the Crinoids the apical system serves as the functional sensory system, and that the radial ectoneural cords are subsidiary. He therefore argues that the apical nervous system of the Crinoid is not strictly comparable to that of the starfish in which the system is entirely motor in function, and comes to the conclusion that the apical system of the Asteroids has no homologue in other Echinoderms.

Physiology of the nervous system

Extensive investigations have been carried out by Uexküll[2] and others on the physiology of the nervous system of the Echinoidea. Uexküll has shown that the spines, pedicellariae, tube-feet, and the lantern are all controlled by the nervous system, and that these organs react in two opposite ways according as the stimulus is weak or strong. Thus the spines bend away from a point of strong stimulation but bend towards it when the stimulation is weak. Uexküll thinks that these opposite reactions are due to the fact that the nervous system exercises two different effects on the muscles, according as the stimulation is strong or weak. He thinks that the nervous system exhibits what is called a "*tone*" in the case of muscles. In a muscle the "*tone*" denotes merely the amount of chronic contraction. The more the "tone" in a muscle, the less responsive it is to stimuli which tend to bring about its contraction. The term as applied to the neurones means a condition in which they are not receptive to small stimuli but keep up a condition of tone in the muscles they control; in fact, it is by determining the tone of the muscles that the tone of the neurones is measured. The more the tone in the neurones, the less is their power to bring about movements in muscles. Another way of measuring the tone of a neuron would be to estimate the amount of stimulus necessary to excite the neuron.

1 Smith, J. E.——"On the nervous system of the starfish *Marthasterias glacialis*", Phil. Trans. Roy. Soc. B., vol. 227, 1937.

2 Von Uexküll——"Die Physiologie des Seeigelstachels", *Zeit. fur. Biol.*, Bd. XXXIX, 1900.

The muscles suffer loss of tone when they relax and there is a corresponding reduction in the tone of neurones controlling them. Similarly, loss of tone in the neurones would lead to the relaxation of muscles under their control. Bending of spines towards one side as a result of a gentle stimulation brings about a contraction of the muscles on the side towards which the spines are bent and a simultaneous relaxation of the corresponding muscles of the opposite side. According to Uexküll's view, bending of a spine would result in an acquisition of tone on one side and a loss of it on the other, so that the stretched side becomes more susceptible to stimuli, while there is a loss of this power on the contracted side. This leads to a readiness of the stretched muscles to react quickly.

In this way Uexküll tries to interpret the various movements of the animal brought about by the action of spines. The central nervous system accordingly would become a storehouse of "tone" rather than a controlling centre in the sense in which it is understood in the case of higher animals. But if the central nervous system is cut or otherwise badly damaged, the control of tone in the muscles is gradually lost, and with it the power of co-ordinated action.

It cannot be said that this explanation of Uexküll will account for all the activities of a sea-urchin or a starfish. There is in some measure an influence of the "whole" on its component parts. When a starfish is turned on its back, it endeavours to right itself and the same is true of a sea-urchin. The tube-feet are expanded in all directions seeking for something to hold on to, but eventually it is pulled over towards one side. Loeb interpreted this as a question of "pull devil pull baker", i. e., whichever tube-feet pulled hardest gained the day. But Jennings has shown that this is not the case. After the tube-feet of all the rays have become attached, a "righting impulse" passes over the animal, i. e., the starfish "makes up its mind", so to speak, to right itself and then the tube-feet of certain of the rays *let go their hold*, leaving the tube-feet of the other rays to control their movements, and then the starfish yields to the pull of these rays and rights itself. Preyer finds that the brittle-stars employ different kinds of dodges if their arms are encumbered by rubber-bands, but this degree of intelligence is not observed in other classes of Echinoderms.

CHAPTER IX

THE RECEPTOR ORGANS

The receptor organs are poorly developed. The tube-feet, pedicellariae and the smaller spines are all highly sensitive to touch and are to be regarded as *tactile receptors*. The tube-feet have a rich nerve-supply (fig. 30), while the pedicellariae and spines are provided with special aggregations of nervous tissue. Judging from Smith's description of *Marthasterias glacialis*[1] it seems probable that the tube-feet and pedicellariae have their own independent action systems and their own reflexes, i. e., they can act without the intervention of the circum-oral ring of the nervous system. The buccal tube-feet are highly sensitive and Chadwick mentions the occurrence of a cushion of nervous tissue in relation with each sucker in *Echinus multituberculatus*. MacBride interprets such suckers in the just metamorphosed larva of *Echinus esculentus* as being larval receptor organs. Such organs are also present in the larvae of *Salmacis bicolor*.

The *terminal tentacle* lying at the end of each radial water-vessel and projecting slightly on the ocular plate bears a pigment spot at its tip (fig 36).

Sphaeridia (Page 16) which were discovered by Sven Loven are present in all Echinoids except in the genus *Cidaris*. They are minute, hard, and globular calcareous structures of a glassy appearance. Each sphaeridium consists of a head and a short stalk by means of which it is attached to a minute boss or swelling on the ambulacral surface. Externally each is covered by a layer of ciliated cells which are generally cubical but become elongated near their bases. Beneath the ciliated epithelium lies a nerve-plexus which is connected with a nerve-ring at the base of the sphaeridium. Within the cavity of each sphaeridium there is a calcareous fenestrated skeletal piece connected with the stalk (fig. 37). The sphaeridia are capable of easy movement and in forms like *Spatangus purpureus* there is a muscle-sheath surrounding the stalk of each sphaeridium. They usually project freely in the regular urchins but may occur in depressions as in *Salmacis*, or in completely closed grooves as in the irregular forms. From their occurrence near the peristome

1 Footnote 1 on Page 50.

they were believed to be olfactory or gustatory in function, but we are now almost certain that they are balancing organs like the *statocysts* of Coelenterates. As the urchin crawls over uneven rocky surfaces, the heavy heads of sphaeridia incline now this way and then that, according to whether the urchin sways to one side or to another, and thus cause a strain on the nervous layer on the side towards which the sphaeridium is inclined. In this manner the animal is made aware of its relative position in regard to the vertical.

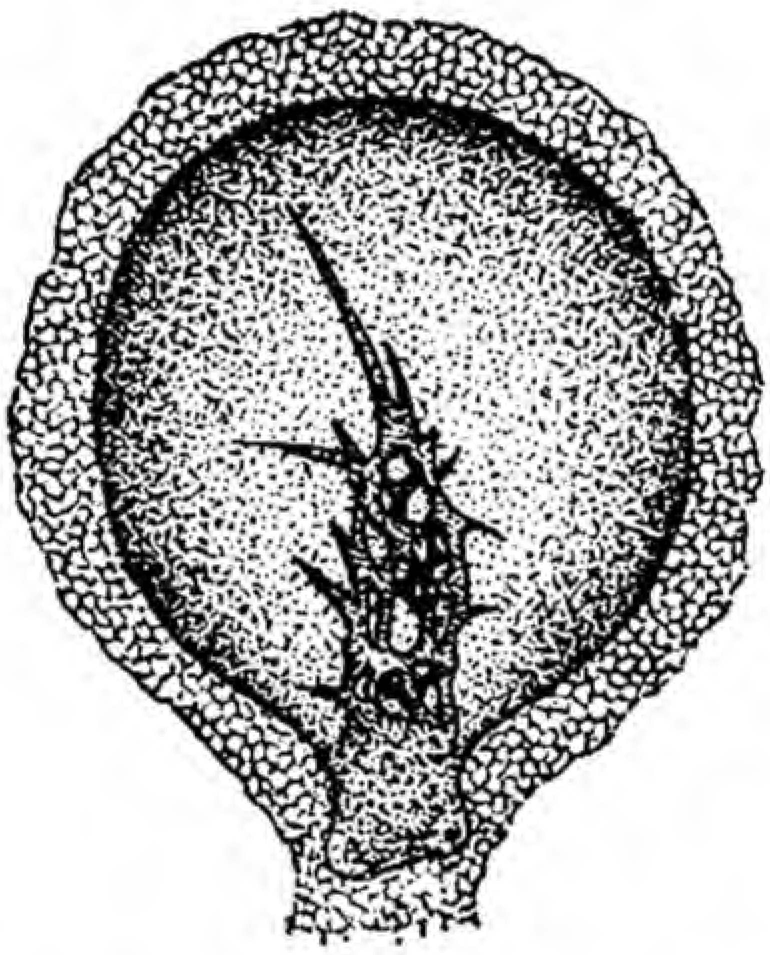


Fig. 37—A sphaeridium in optical section. (× cir. 225)

Special visual organs are absent in *Salmacis* but in *Diadema setosum*, a common form described from Ceylon, numerous shining eye-spots have been noticed all over its surface. As regards the pigment-spots on the ocular plates (fig. 36), it should be remembered that they are homologous with the regular eyes at the bases of the ocular tentacles of the starfish. If the ocular tentacles of a starfish are cut off, it is unable to distinguish light from darkness. It seems natural to suppose that some vestige of this function resides in the ocular spots of sea-urchins, but it is doubtful whether it is effective.

CHAPTER X

THE REPRODUCTIVE SYSTEM

The sexes are separate. There are five bunches of interradially placed *gonads* hanging downwards into the perivisceral cavity from the apical part of the test (figs. 34 and 38) by means of coelomic membranes. When mature the gonads are orange-coloured in the female but whitish in the male. Each gonad consists of a large number of branching tubules, each of which contains a minute ductule; several of these ductules join together to form a main duct (fig. 34); the five main

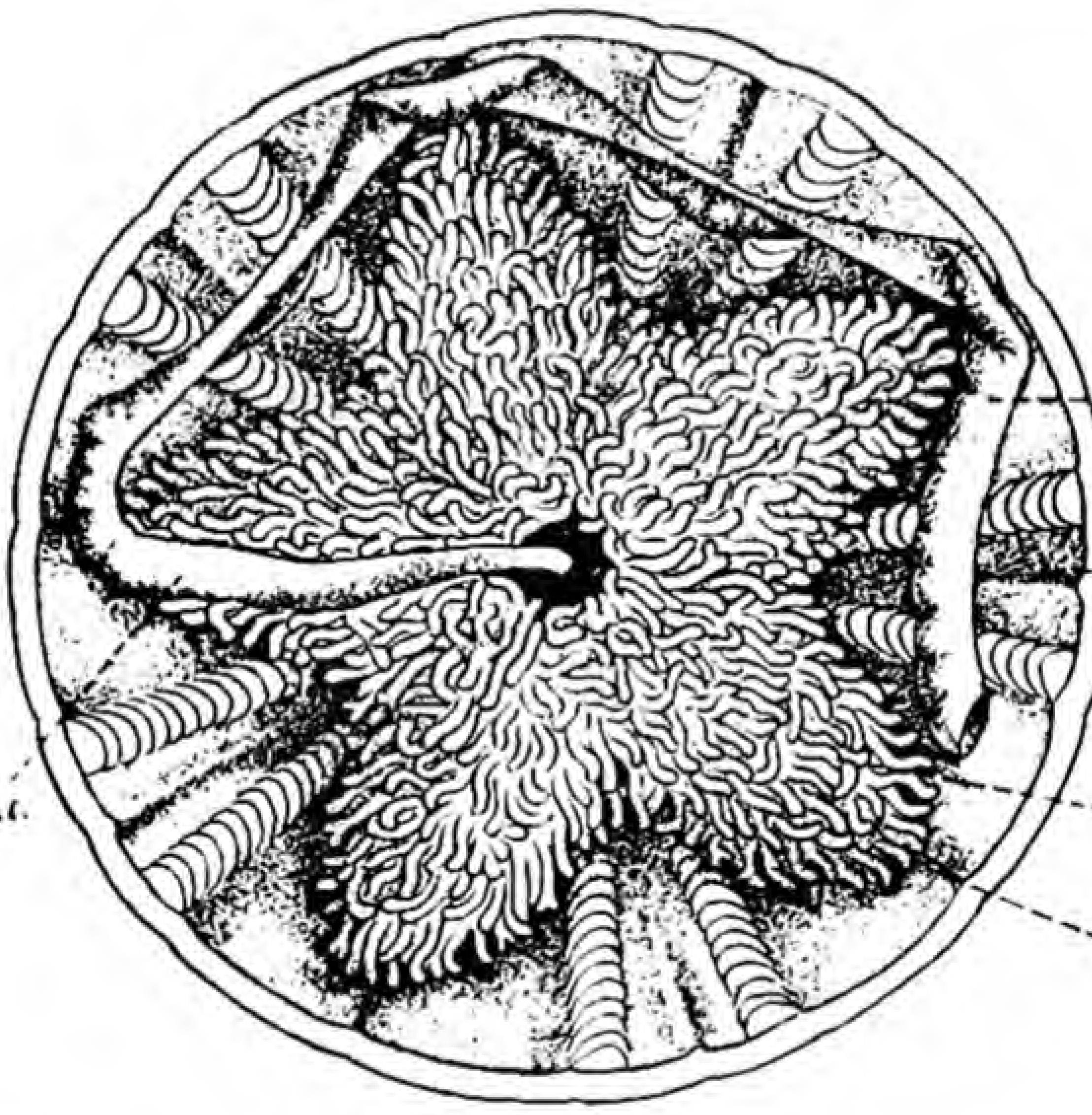


Fig. 38—Inner view of the aboral part of the animal showing the disposition of the gonads. *amb.*, ambulacrum; *g.*, gonad; *i. amb.*, inter-ambulacrum; *rect.*, rectum; *sup. s.*, superior spiral. (× cir. 1½)

ducts pass upwards to perforate the aboral circular coelom and reach the outside through the genital pores on the basal plates (fig. 34), and finally open at the tips of minute papillae. It was formerly believed that the aboral ring-coelom acted as a connecting tube between the five genital ducts, but it has now been definitely established that the coelom contains a pentagonal genital rudiment, from which the five genital rachides are given off, and that each rachis is connected with a gonad. The genital papillae occur in several forms, e. g., *Echinus acutus*,

Dorocidaris papillata and others; in *Dorocidaris papillata* they are said to be 10 mm. long. It is believed that the genital products are pressed out by the muscular contractions of the outgoing ducts. The walls of the genital tubules (fig. 39A) consist of a coelomic epithelium on the outside, a middle layer of muscle-fibres interspaced with connective tissue, and lastly, an inner layer of germinal cells. The walls of the genital ducts, both main and accessory, as also the bases of the genital tubules are strengthened by C-shaped spicules, but their terminal portions are free from them. The germinal layer consists of almost similar cells in the young condition; but differentiation takes place later into the male and female elements. Cells destined to give rise to oogonia increase rapidly in size, while the surrounding cells undergo degeneration and become converted into nutritive bodies which

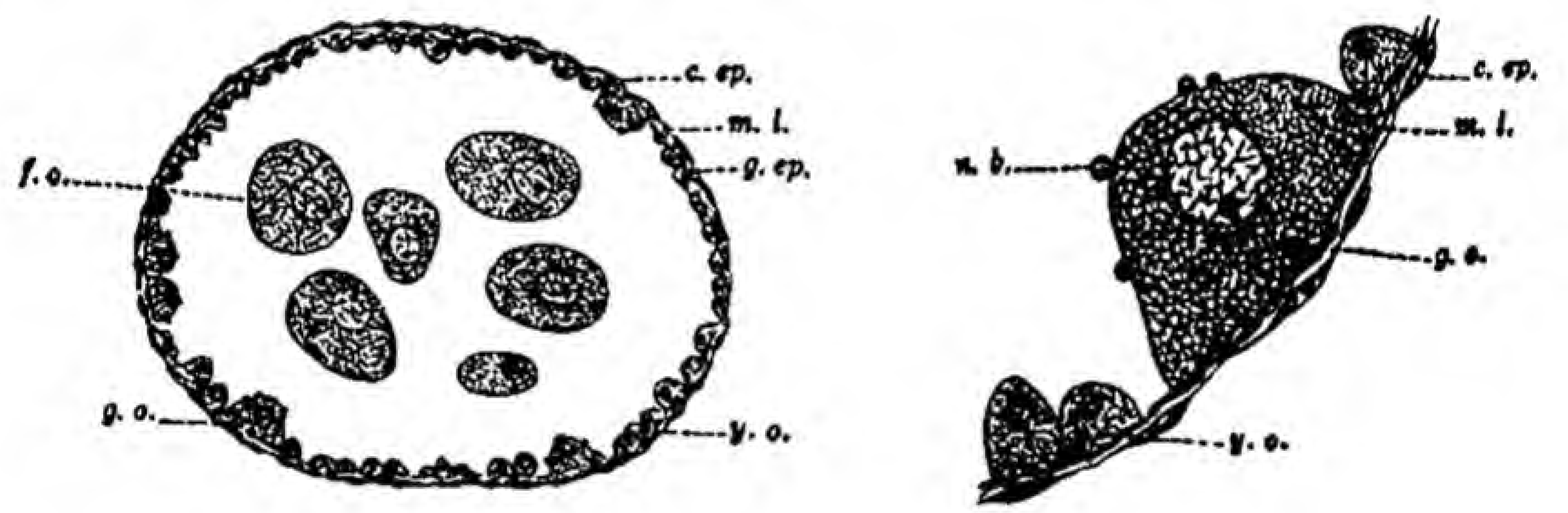


Fig. 39—A. Section of an ovarian tubule (× cir. 28). B. Part of the wall of an ovarian tubule (× cir. 1000). *c. ep.*, coelomic epithelium; *f. o.*, free ovum; *g. ep.*, gonadial epithelium; *g. o.*, growing oocyte; *m. l.*, muscular and connective tissue layer; *n. b.*, nutritive bodies; *y. o.*, young oocyte.

are grouped around the growing oocytes (fig. 39B). The nutritive bodies of *Salmacis* are of two types, lipoidal and albuminous, according to the nature of the food-material contained in them[1]. A similar phenomenon has been observed in an American form *Echinometra lacunter*[2]. In the fully ripe condition, the gonads fill up almost the whole of the upper part of the test and press against each other and may reach downwards almost up to the level of the Aristotle's lantern.

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1 Subramaniam, M. K.—"A cytological study of the structure and formation of nutritive bodies in *Salmacis bicolor*". Zeit. Wiss. Zool. Bd. 146, 1936.

2 Tennent, D. H., Gardiner, M. S., and Smith, D. E.—"A cytological and biochemical study of the ovaries of the sea-urchin *Echinometra lacunter*". Carn. Inst. Wash. Publ. 413, 1931.

The eggs are small, about 0.1 mm. in diameter, and are very numerous. It has been estimated that a female *Echinus esculentus* produces as many as 20 million eggs in a season. At the time of breeding in *Salmacis*, the eggs, as they come out of the genital pores, from five cloudy-white masses (fig 40) at the aboral pole of the animal. They are discharged into the sea where they are fertilized.

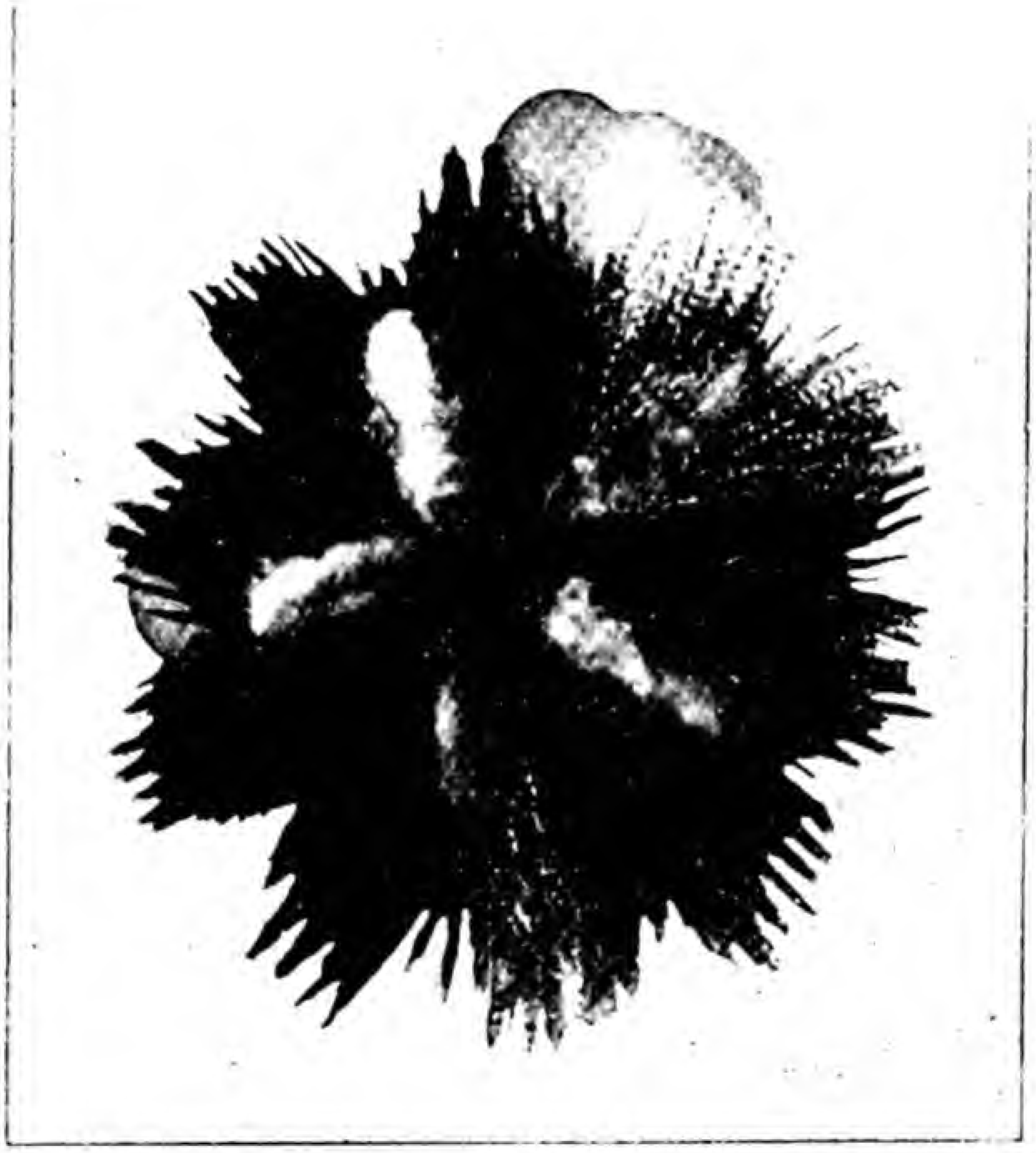

Fig. 40—Photograph of a female *Salmacis* in the act of breeding.

CHAPTER XI

THE DEVELOPMENT

Soon after insemination a fertilization membrane is formed round the egg. The first cleavage is meridional and divides the egg into two blastomeres; the second division is also meridional, but at right angles to the first, and results in the four-celled stage which is reached in about two hours. The third division is equatorial and gives rise to the eight-celled stage which consists of four small upper cells and four lower cells. The 16-, 32-, and 64-celled stages are soon passed through, and the

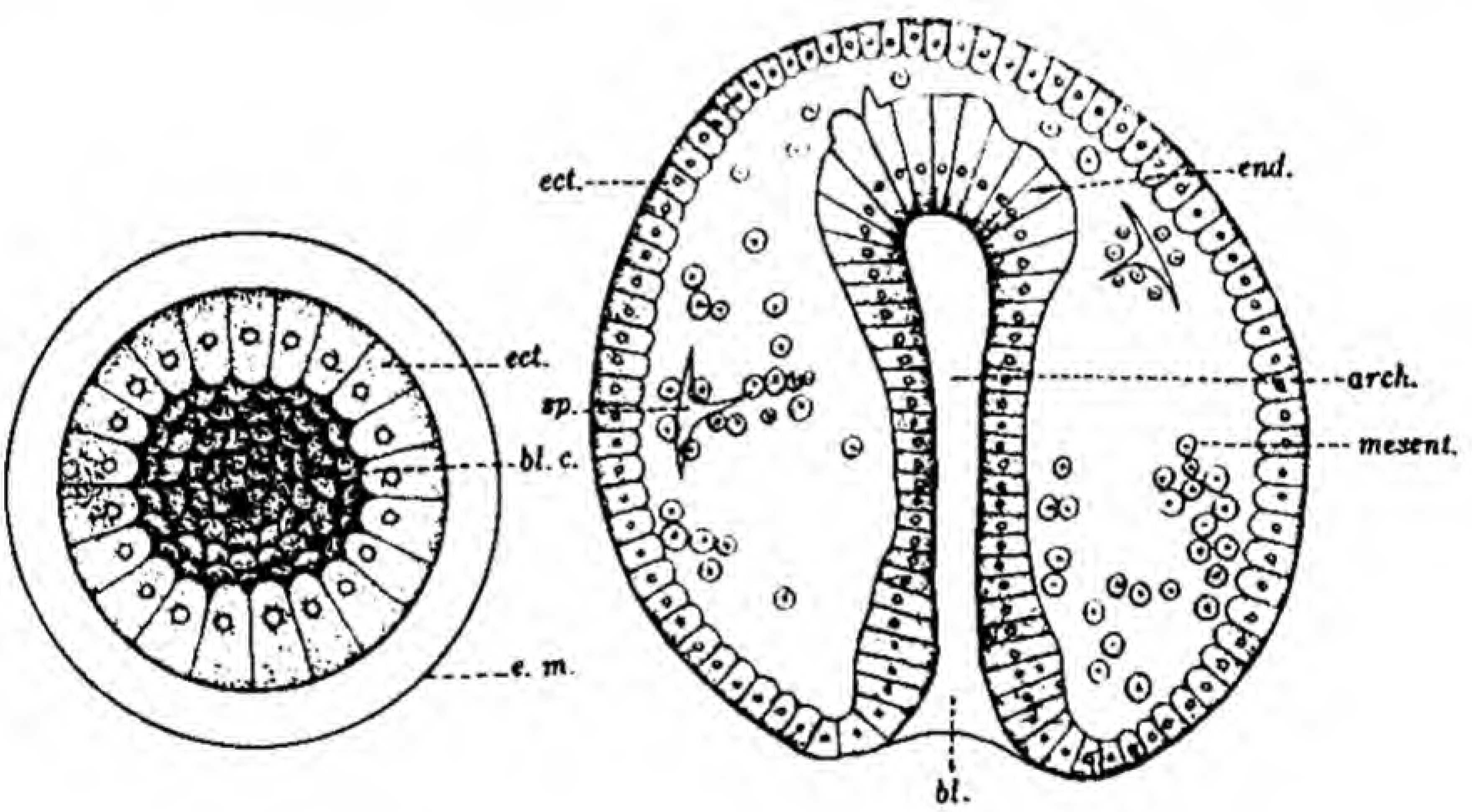

Fig. 41 Fig. 42

Fig. 41—Blastula, eight hours old. *bl. c.*, blastocoele; *ect.*, ectoderm; *e. m.*, egg-membrane. (× cir. 75)

Fig. 42—One day old gastrula in optical section. *arch.*, archenteron; *bl.*, blastopore; *ect.*, ectoderm; *end.*, endoderm; *mesent.*, mesenchyme; *sp.*, spicule. (× cir. 250)

multicellular hollow blastula stage is reached in about eight hours (fig. 41). Mesenchyme cells are now budded off into the cavity of the blastocoele and soon an invagination becomes evident at one pole which leads to the formation of a gastrula in about 23 hours (fig. 42). The growing embryo now consists of an outer layer of almost similar cells, the *ectoderm*, and an inner tube-like structure,

the *archenteron* formed of *endoderm*. In the disappearing blastocoele between the ectoderm and the endoderm lie a large number of mesenchyme cells some of which are seen to group themselves together on either side of the archenteron. These cells secrete the *larval skeleton* in the form of a tri-radiate spicule on either side (fig. 42). These two spicules clearly lay down the initial bilateral symmetry which is a conspicuous feature of the Echinoid larva. The larva by this time becomes helmet-shaped and indications of the post-oral arms appear during the middle of the second day, and before the day is completed, these arms are fully established. A stomodaeal pit begins to form at the apical pole which, on

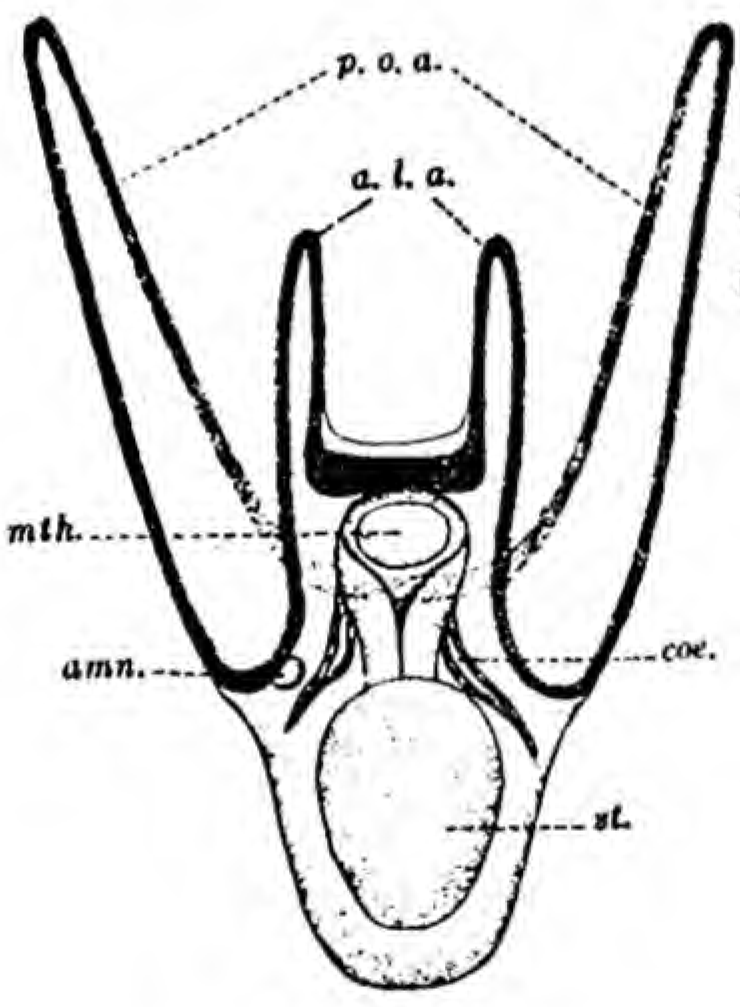

Fig. 43

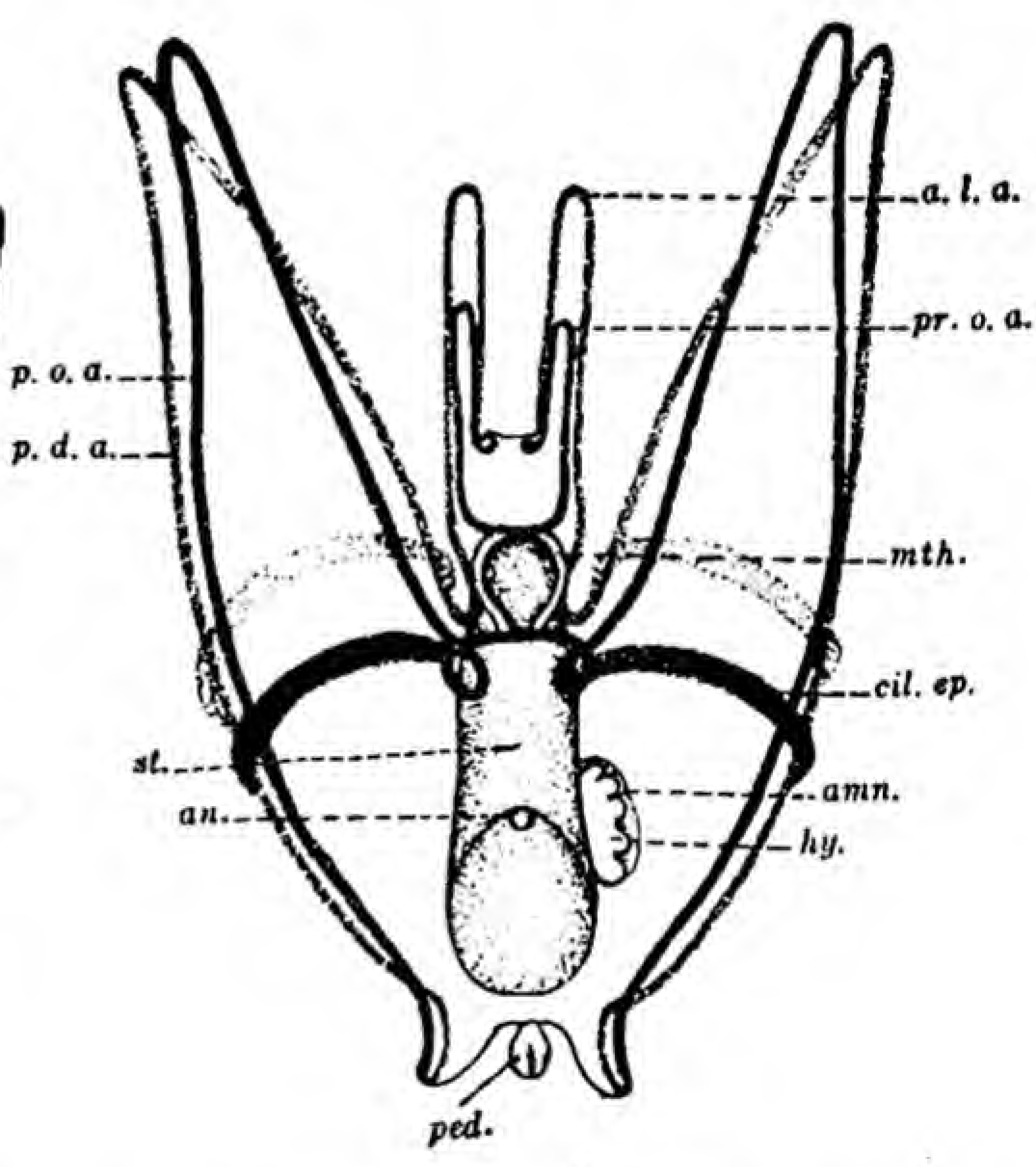

Fig. 44

Fig. 43—Dorsal view of the first pluteus stage, three days old, with four arms. *a. l. a.*, antero-lateral arms; *amn.*, amnion; *coe.*, coelom; *mth.*, mouth; *p. o. a.*, post- oral arm; *st.*, stomach (× cir. 160)

Fig. 44—Ventral view of a larva, fourteen days old. *a. l. a.*, antero-lateral arm; *amn.*, amnion; *an.*, anus; *cil. ep.*, ciliated epaulette; *hy.*, hydrocoel; *mth.*, mouth; *p. d. a.*, postero-dorsal arm; *ped.*, pedicellaria; *p. o. a.*, post-oral arm; *pr. o. a.*, pre-oral arm; *st.*, stomach. (× cir. 58)

growing deeper, approaches the front end of the archenteron, impinges on it, and divides the already formed coelom into right and left halves. Soon, a rupture of the intervening layers takes place and the stomodaeum establishes a connexion with the archenteron. The anal opening also now becomes clear. On the left, an ectodermal invagination leads to the formation of a sac, the *amnion*, which indicates the future oral surface of the larva.

Our knowledge of the development of the coelom in sea-urchins is mainly derived from the work of MacBride on the British forms *Echinus esculentus* and *Echinus miliaris*. The more important features of the development of the coelom may be briefly stated here. The coelomic rudiment, after being pinched off from the anterior end of the archenteron, becomes constricted along its median line giving rise to right and left coelomic sacs of about equal size (fig. 43). These sacs grow backwards and upwards. The left coelomic sac becomes transversely divided in the middle and thus leads to the formation of an anterior and a posterior coelom on the left side. The same process is repeated on the right side slightly later. The left anterior coelom soon sends upwards a finger-shaped process which, on coming into contact with the ectoderm, fuses with it and finally acquires an opening to the exterior. This opening is known as the *primary water-pore*. The front part of the left anterior coelom undergoes a swelling which persists in the adult as the *madreporitic ampulla* and *axial coelom*. The posterior end of the left anterior coelom constricts off a sac, the *hydrocoel*, which forms the rudiment of the water-vascular system. The connecting tube between the anterior swelling and the posterior hydrocoel remains as the *stone-canal*, which establishes a connexion with the outside through the madreporitic ampulla and the water-pore. The hydrocoel during development is pierced by the oesophagus and thus forms the *water vascular ring-canal* which sends out the five *radial water-vessels*. The *lantern-coelom* is formed from five evaginations (dental sacs) of the left posterior coelom, the teeth and jaws being formed in the walls of these *dental sacs*. The *aboral circular coelom*, the *genital rachides* and the *gonads* are coelomic in origin and are also developed out of the left posterior coelom. Sometime later, a bud, called the *pericardial sac*, is separated off from the hind end of the anterior division of the right coelom; this bud acquires a dorsal position in the adult and comes to lie almost immediately beneath the madreporitic plate and is known as the *madreporic vesicle* or *dorsal sac*. The pericardial sac is the homologue of the *vibratile sac* of the *Tornaria larva* of *Balanoglossus*. In the larva of *Echinus* this sac is pulsatile and its pulsations have been observed and counted by Murti. These pulsations have not, however, been noted in the larva of *Salmacis*. The anterior end of the right anterior coelom disappears. The right and left posterior coeloms are of unequal size and give rise primarily to the *perivisceral cavity* of the adult urchin.

Long before the post-oral arms are completed, in fact, during the third day after fertilization, a second pair of arms, the *antero-laterals*, have appeared and the larva assumes the "*pluteus*" shape (fig. 43). There is a single ciliated band which runs along the borders of the two pairs of arms. All the arms are supported by well developed calcareous supporting rods. The alimentary canal now consists of the *pharynx*, *oesophagus*, *stomach* and the *intestine*.

As the larva enters its second stage of development the remaining pairs of arms, the *postero-dorsal* and *pre-oral*, are formed (fig. 44). *Ciliated epaulettes*, which are portions pinched off from the bottom of the continuous ciliated band at the bases of four of the arms, are formed during this stage. Soon they

Fig. 45—A just metamorphosed *Salmacis*. (× cir. 50).

look like ear-shaped structures and become the essential organs of locomotion of the rapidly developing *echinopluteus larva*. In *Salmacis* (fig. 44) the two anterior ciliated epaulettes alone are present, whilst in other forms like *Echinus esculentus* the two posterior epaulettes are also formed. The first pedicellaria (fig. 44) appears in the form of a knob in which a large number of mesodermal cells can be observed to accumulate. By the fourteenth day, the knob has split into three jaws, and the ophicephalous type of pedicellaria stands revealed. By about the nineteenth day two more pedicellariae of the same kind are added. Now the amnion grows bigger and occupies a position above the hydrocoel and the rapidly developing primary tentacles. The latter push

themselves into the base of the amniotic cavity which later becomes the ambulacral surface. The floor of the amniotic cavity and the outer surface of the hydrocoel become greatly depressed and the *oral disc* of the young sea-urchin is built up. This compound structure is called the *Echinus-rudiment.* The larva by this time becomes very heavy and sinks to the bottom. There is no fixed stage during development. The stomach is blue in colour and becomes pushed to the right side. The metamorphosis now commences. The larval arms and their calcareous supports are rapidly devoured by phagocytic activity and are finally lost. The amoebocytes of the mesoderm play an important part during

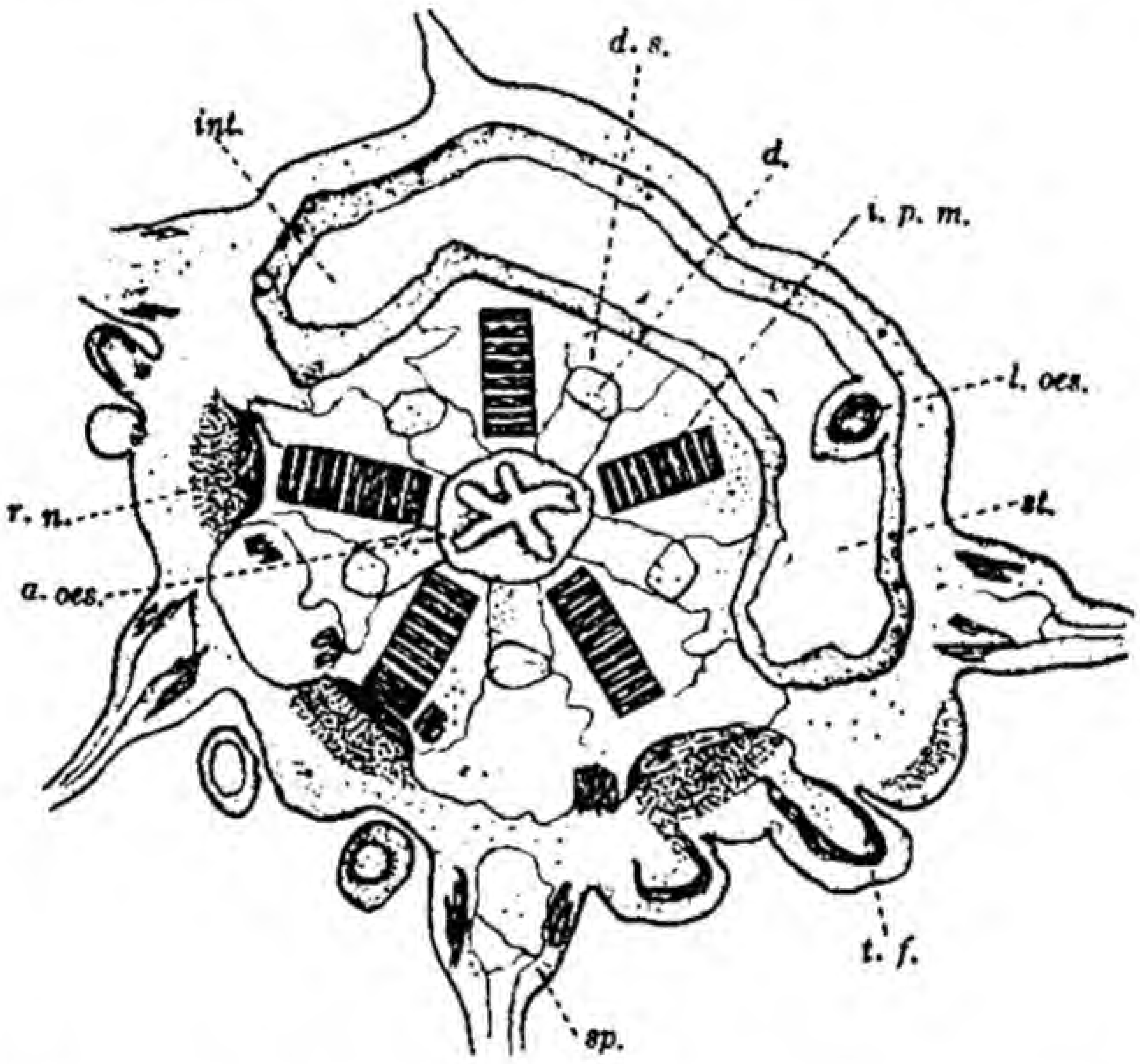

Fig. 46—Horizontal section of a just metamorphosed *Salmacis*. *a. oes.*, adult oesophagus; *d.*, tooth; *d. s.*, dental sac; *int.*, intestine; *i. p. m.*, inter-pyramidal muscles; *l. oes.*, larval oesophagus; *r. n.*, radial nerve; *sp.*, spine; *st.*, stomach; *t. f.*, tube-foot. (× cir. 105).

metamorphosis. They engulf and absorb, by intra-cellular digestion, several larval organs. The destructive activity of these cells is clearly seen when the cells associated with ciliary bands are gradually engulfed. In fairly transparent larvae the process of engulfing and digestion is easily followed. In later stages, the primary tube-feet break through the amniotic floor and begin to project; quadrangular spines and ordinary smooth spines appear and the young *Salmacis* creeps at the bottom by means of its spines and tube-feet (fig. 45). The adult mouth appears a few days later. As yet only the first part of the alimentary

canal is formed, but in a fortnight's time the second coil is also formed (figs. 46 and 47). In about three months when the young *Salmacis* is 4.5 to 6 mm. in diameter, the adult anus is formed and the animal is quite like the adult, except in size and in the absence of reproductive organs. Specimens of *Salmacis* reared in the laboratory grew to a size of 15 × 9 mm. in one year but were still immature.

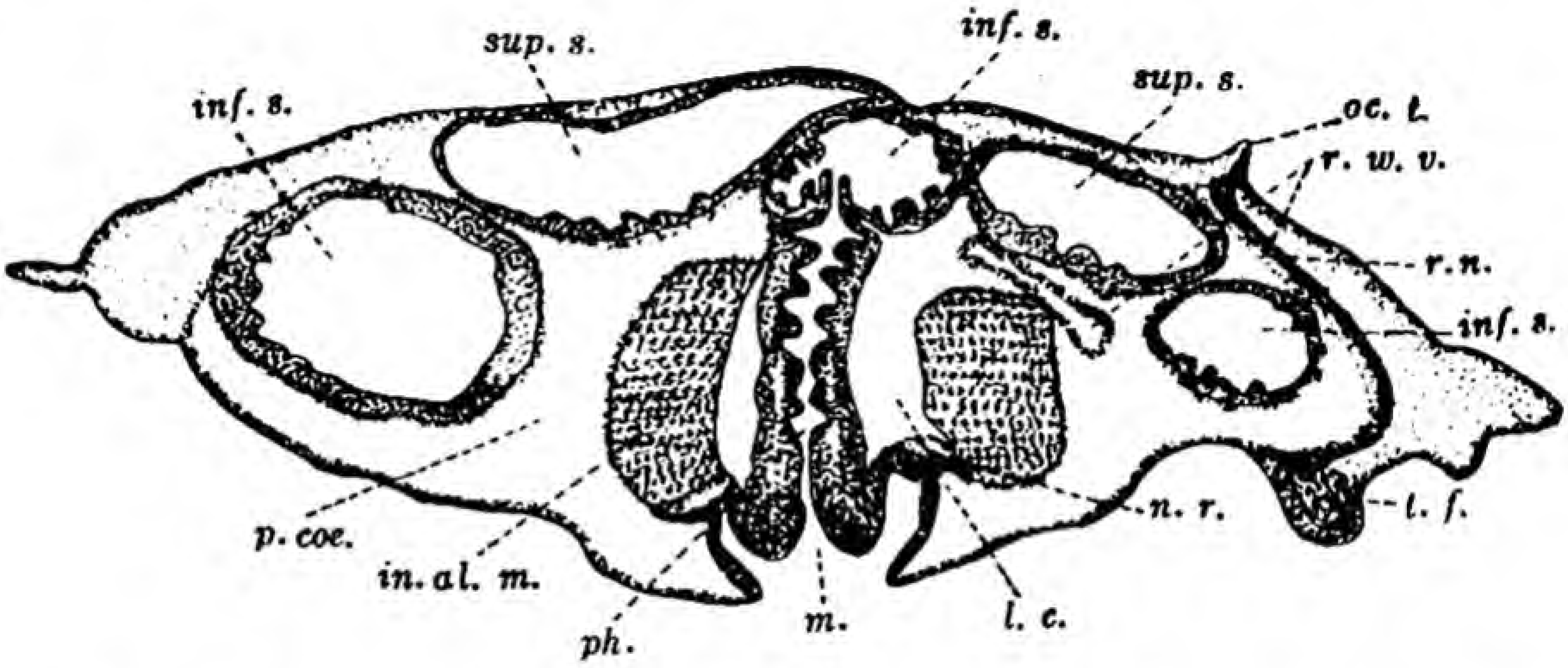

Fig. 47—Vertical section of a 45 days old urchin. *in. al. m.*, inter-alveolar muscles; *inf. s.*, inferior spiral; *m.*, mouth; *n. r.*, circum-oral nerve-ring; *ph.*, pharynx; *r. n.*, radial nerve; *r. w. v.*, radial water-vascular canal; *sup. s.*, superior spiral; *t. f.*, tube-foot. (× cir. 70)

CHAPTER XII

BIONOMICS

Sea-urchins are entirely marine, none of them having been recorded from fresh or brackish water. They move by means of their spines and tube-feet. The regular urchins are rock dwellers, while the cake- and heart-urchins burrow in sand. The regular forms feed mainly on algae (sea-weeds) as also on small animals. Broken shells and parts of the soft body of *Balanus* have been found in the intestine of *Salmacis bicolor*. The heart-urchins feed on small mussels, gastropods, etc., which are taken up from the surface of the bottom deposit by means of the long tube-feet attached to the anterior petal. The cake-urchins swallow large quantities of mud from which they extract what little organic matter may be present. Dohrn has described that *Sphaerechinus* and *Strongylocentrotus* are carnivorous and have the peculiar habit of masking their approach by carrying a number of mussels on their backs. They have been observed to kill and feed upon *Squilla mantis*.

No actual data regarding the rate of growth are available, but there is reason to think that the growth of Echinoids is rather slow. The British form *Echinus esculentus* is said to reach its full size in about four years, while *Stylocidaris* takes about two years to reach sexual maturity. It has been proved by work at the Plymouth laboratory that *Echinus miliaris* becomes sexually mature within a year of its existence[1].

After three and a half months of growth under tropical laboratory conditions, *Salmacis bicolor* often shows a maximum test diameter of 11 mm. A young specimen of *Salmacis* measuring 22 mm. across from the Madras Harbour was found to be immature.

Echinoids have their external surface free from incrustations. A few crustaceans, chiefly Amphipods, have been observed

1 Professor MacBride gives me the following information:—

"In 1908 as a result of a terrific explosion of Mount Vesuvius which blew into the air an enormous amount of scour, the whole of the bottom fauna of the Bay of Naples was destroyed. The three regular urchins of the Bay, *Strongylocentrotus lividus, Echinus microtuberculatus*, and *Sphaerechinus granulatus*, were found fully grown and sexually mature one year after the eruption, from which Lo Bianco deduced that they grew to full size in one year".

to live amongst the spines of *Salmacis*. Some workers have reported that *Zebrida adamsii*, a small crab, is of common occurrence among the spines of tropical Echinoids. Eulimid Gastropods also occur in Echinoids. Among the long spines of a tropical form *Diadema*, small fish and shrimps have been noticed to take shelter. Several ciliates are known to occur in the alimentary canals of regular urchins.

Sea-urchins are eaten by all the lower classes along the coast of the Mediterranean and also at Madras, Tuticorin, Cape Comorin, and other places. It is the ripe gonad that is edible.

Lunar periodicity in reproduction occurs in certain Echinoids, as for instance in *Centrechinus* (*Diadema*) *setosus* living in the Red Sea. Munro Fox[1] mentions that during the breeding period, i. e., July, August, and September, spawning takes place at each full moon; a fresh crop of genital products is developed each time, the same individual becoming sexually mature at consecutive lunar periods. Many of the European species show definite breeding seasons, but there does not appear to be any definite sexual periodicity in *Salmacis bicolor*, since ripe individuals can be obtained throughout the year from the Madras Harbour, where the temperature of the seawater varies during the year from 24° to 30° C. It is, however, very probable that there is intensive breeding during the rainy months. A shoreward migration of *Echinus esculentus* at the spawning period has been observed on the west coast of England. As a rule, urchins dislike rough weather and crawl downwards when a storm comes on. In the Madras Harbour, the fact that small individuals are never encountered near the surface of the sea indicates that the young immature forms inhabit the bottom and crawl up only when they are sexually mature.

1 Fox, H. M.—"Lunar Periodicity in Reproduction", Proc. Roy. Soc., B., vol. 95, 1924.

CHAPTER XIII

DIRECTIONS FOR PRACTICAL WORK

When available, living specimens of *Salmacis* should be preferred and examined in dishes containing seawater. If live specimens are not available, specimens preserved in 5% formol should be examined.

External Characters

With the help of figs. 1 to 9, examine the following external characters:

1. The shape of the animal, its *oral* and *aboral* ends, and the *spines*. The structure and attachment of a spine, as shown in fig. 3, should be made out with a hand-lens. Primary, secondary, and tertiary spines should be carefully distinguished.
2. The ten rows of *tube-feet* with suckers at their ends, and the ambulacral and inter-ambulacral zones.
3. The *peristome*, the *mouth*, the five white *teeth*, the five pairs of *buccal tube-feet* and the minute *pedicellariae* round each of them, the *peristomial membrane* and the inter-ambulacral tufts of *branchiae*. It will be instructive to make a stained balsam mount of a branchia and compare it with fig. 35. Bihamate spicules and fenestrated plates can be made out in the branchiae (fig. 35).
4. The *periproct* with the slightly excentric *anus* and the thick *madreporitic plate*.
5. The *bigger gemmiform pedicellariae* at the aboral pole, and the *smaller gemmiform*, *tridentate*, *ophicephalous*, and *triphyllous pedicellariae* scattered all over the body. If the specimen is alive, note the opening and closing of the blades of pedicellariae. But if a preserved specimen alone is available, scrape a portion of the surface of the animal on to a watch glass, pick out the pedicellariæ and examine under a microscope. Balsam mounts should be made of each of the five types of pedicellariae and compared with fig. 7. In order to examine the blades of different kinds of

pedicellariae, as shown in fig. 8, the pedicellariæ should be treated with a 10 % solution of caustic potash and the jaws mounted in glycerine or balsam.

6. *Sphaeridia.* With a strong lens look for the sphaeridia in the ambulacral areas just outside the peristomial region; they lie in shallow pits and look like minute glassy beads (fig. 9). Remove a few and make an unstained balsam mount and compare it with fig. 37.

The Skeleton

The skeleton of the test can be prepared from a fresh or preserved animal by washing it in water and allowing it to dry in the sun. Repeated washings with freshwater and drying for several days in the hot sun will bleach the shell. For a careful study of the skeletal plates, the shell should be treated with a 10 % solution of caustic potash, when the pieces can be separated off easily.

1. Examine a dry piece of test which has been treated with caustic potash. Note the difference in outline between the *median suture* separating the two rows of plates of an ambulacrum and the *outer suture* between a row of ambulacral and a row of inter-ambulacral plates (fig. 12).

2. Examine the outer margins of the ambulacral zones for the *double pores* (*pore-pairs*) for the tube-feet (fig. 12).

3. In a well-cleaned ambulacral plate, examine its three components, the two *primary plates* and a *demi-plate*, as shown in fig. 12.

Internal Anatomy

In order to examine the internal anatomy of the animal, it is best to make a circular cut across the broadest part of the shell and divide it into an upper and a lower half.

1. In the lower half of the urchin, note the following structures:—

The *Aristotle's lantern* with its component pieces (figs. 17, 18 and 19), the *muscles* which move them (fig. 18), the *water-vascular ring*, the *Polian vesicles*, and the five projections of the *lantern-coelom* (figs. 26 and 36). The lantern of Aristotle should be removed and cleaned, and its various ossicles identified with the help of fig. 17. Observe also the *perignathic girdle* around the lantern and its components, the *auricles* (fig. 18).

2. On the inner surface of the ambulacral zones note the *radial water-vessels*, the *transverse vessels* and the *ampullae* (figs. 26 and 27).

3. Examine the *pharynx* projecting out of the centre of the lantern-apparatus and its continuation into the *stomach* or *inferior spiral* of the alimentary canal having a festoon-like arrangement (fig. 19).

4. Note the *stone-canal* and *axial coelom* running along the first part of the inferior spiral, and also the position of the *siphon* (fig. 36).

5. In the upper half of the urchin, note the *superior spiral* or the *intestine*, the direction of its course, and the difference in colour between the inferior and superior spirals (fig. 20).

6. Note the attachment of the five *gonads* to the top of the inner surface of the upper half of the shell. Observe the gonadial ducts and the connecting *aboral ring-coelom* (fig. 34).

Histology of the Viscera

For sectioning the soft parts, it is advisable to fix the required material in Bouin's fluid for 5 to 10 hours. The acetic acid in the fixative will dissolve most of the spicules which are present in abundance in the soft parts of the animal. The material may then be transferred to 70 % alcohol, dehydrated, and paraffin sections made in the usual manner. For sectioning the test, it should be fixed in formol and decalcified in formol-nitric acid mixture. Intestinal contents are best studied in the fresh condition.

Developmental Stages

For a study of developmental stages, it is best to fertilize the eggs artificially in jars of clean seawater. Ripe individuals are easily obtained at Madras throughout the year. A small piece of the slightly orange-coloured mature ovary is wrapped in a piece of fine muslin and shaken in a jar containing seawater, when the eggs escape in thousands into the water. An emulsion of spermatic fluid can be made by squeezing the testis-tubules in a watch glass containing clean seawater. Only a few drops of the emulsion are added to the jar containing the eggs. After the eggs have fallen to the bottom, the water at the top should be pipetted off and fresh seawater added. Overcrowding of eggs should be avoided. When the free-swimming larvae float up, they should be removed and distributed over a number of jars containing fresh seawater.

In India developing eggs are difficult to rear in the laboratory on account of the high temperature; the culture jars should, therefore, be kept in a spacious room and the windows and doors kept open day and night. As a further precaution, it is highly desirable to cool the jars, which is done by wrapping a piece of ordinary cloth round them and allowing the corners of the cloth to dip in vessels containing water. By this means the temperature is kept down by 4° to 5° C. It has been found that in Madras a temperature of 25° to 27° C is the most suitable for growing larvae. They may be fed either on diatom cultures obtained from Plymouth or by merely adding fresh seawater filtered through a piece of coarse muslin. The latter method was found to be very effective and the larvae were able to obtain their natural food. It is desirable to pick out the larvae by means of a suitable pipette once in two or three days and transfer them to jars containing clean seawater brought from some distance away from the shore. The larvæ are best studied in the living condition. For whole mounts and sections they are fixed in Bouin Duboscq. Double imbedding method is preferable for sectioning the larvae, and staining with Delafield's haematoxylin usually gives good results.

1. Examine the blastulae, the gastrulae, and the first and second pluteus stages (figs. 41-44), and note the number and disposition of the arms, the position of the mouth and anus, the course of the ciliated bands, and other details as mentioned in the text.

2. Examine, if possible, the later larval stages also in the living condition. Note the highly enlarged *amnion* on the left side (fig, 43), the tentacles projecting into the base, the presence of the pedicellariæ at the posterior end, and the gradually diminishing larval arms.

3. Examine the newly metamorphosed urchin (fig. 45), and observe its radial symmetry, primary tube-feet, crowned and ordinary spines, and the absence of the anus.

4. Examine prepared sections for details of the development of the coelom, the hydrocoel, and the alimentary canal.

BIBLIOGRAPHY

1. Aiyar, R. Gopala ... Early development and metamorphosis of the tropical Echinoid *Salmacis bicolor* Agassiz. Proc. Ind. Acad. Sci., vol. 1, No. 11. 1935
2. Bury, H. B. ... The metamorphosis of Echinoderms. Quart. Journ. Micr. Sci., vol. 38, 1895
3. Chadwick, H. C. ... Echinus. L.M.B.C. Memoirs. 1901
4. Clark, H. L. ... Catalogue of the recent sea-urchins in the collection of the British Museum. 1925
5. Duncan, P. M. ... On some points in the anatomy of the Temnopleuridae. Ann. Nat. Hist. Ser. 6., vol. 1. 1888
6. Koehler, R. ... Echinodermes: Fauna de France, 1921
7. Lankester, E. R. ... A Treatise on Zoology: Echinodermata, London, 1900
8. MacBride, E. W. ... The development of *Echinus esculentus* together with some points in the development of *Echinus miliaris* and *E. acutus*., Phil. Trans. Roy. Soc., Ser. B., vol. 195, 1903
9. Idem ... The Echinodermata: Cambridge Natural History, vol. 1. 1909
10. Idem ... The development of *Echinocardium cordatum* Quart. Journ. Micr. Sci., vol, 59. 1914
11. Idem ... A Text-Book of Embryology, vol. 1. Invertebrata, 1914
12. Mortensen, Th. ... The Danish Ingolf Expedition. Echinoidea. vol. 4, pt. 1. 1903
13. Idem ... The Danish Expedition to Siam, 1899-1900. The Echinoidea. 1904
14. Idem ... Contributions to the Study of the development and larval forms, Echinoderms. Pts. I-III. Mem. Acad. Roy. Sci, Let. Danemark., Copenhague. Ser. 9, vols. 4 and 7. 1931—1937
15. Murti, N. N. ... The development and function of the heart and pericardium in Echinodermata. Proc. Roy. Soc. Ser. B., vol. 109., 1932
16. Prouho, H. ... Researches sur le *Dorocidaris papillata*. Arch. Zool. Exper., Ser. 2, vol. 5. 1888
17. Sedgwick, A. ... Students' Text-Book of Zoology, vol. III. 1909

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